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Riparian Buffer Strips: Their Value as Habitat and Movement Corridors for Songbirds in the Boreal Mixedwood Forest of Alberta

by

Craig Stephen Machtans

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

Department of Zoology

Edmonton, Alberta

Spring 1996

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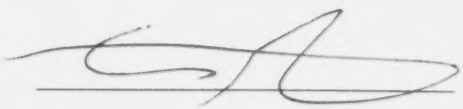

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Riparian Buffer Strips: Their Value as Habitat and Movement Corridors for Songbirds in the Boreal Mixedwood Forest of Alberta* submitted by *Craig Stephen Machtans* in partial fulfillment of the requirements for the degree of Master of Science.

Dr. Susan J. Hannon, Supervisor

Dr. C.A. Paszkowski, Committee Member

Approved On: 22 Jan 1996

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An ecologist must either harden his shell and make believe that the consequences of science are none of his business, or he must be the doctor who sees the marks of death in a community that believes itself well and does not want to be told otherwise.

Aldo Leopold

I do not know what I may appear to the world; but to myself I seem to have been only like a boy playing on the seashore, and diverting myself in now and then finding a smoother pebble or a prettier shell than ordinary, whilst the great ocean of truth lay all undiscovered before me.

Sir Isaac Newton, 1855

Abstract

Many species of forest songbirds are negatively affected by forest fragmentation, a process now occurring in the boreal mixedwood region of Alberta. I studied forest-songbird communities there to: assess the value of forests near watercourses (riparian buffer strips) to songbirds, relative to upland forest; to determine if communities were affected by adjacent harvesting; and to determine if songbirds use and need buffer strips for movement corridors between reserves. I found that forests near watercourses supported more species and individuals than upland forest, both with and without accounting for habitat differences. Songbirds were not severely impacted by the creation of buffer strips. Only the Ovenbird was clearly affected by fragmentation; its spatial distribution in the forest changed and its abundance declined. Songbirds use buffer strips as travel corridors; significantly more forest birds were captured in buffer strips than were seen moving across adjacent clearcuts. Most of the juveniles captured in buffer strips were probably dispersing individuals. The conservation of forest songbirds in the boreal mixedwood would be aided by making buffer strips as wide as possible (>100 m) and by leaving areas of forest connected by corridors.

Acknowledgements

Truly one of the most difficult tasks of a graduate program is writing the thesis acknowledgment section. It is difficult to remember all those who contributed to the successful completion of this work and even more difficult to express the sincere thanks that each person deserves. Bearing that in mind.....

First on the list is my supervisor, Susan Hannon. She injected a mix of supervisory interference to help avoid catastrophes and toe-squishing at critical times, but also gave me a free reign from the very beginning. That freedom was a highlight of my graduate program. Thanks for agreeing to 'can you read this?' time and time again.

Marc-Andre Villard can easily be referred to as my mentor. A colleague, office-mate, field-partner, friend and endless source of information on statistics, ecology and birds, M-A was always there for 'da Craigman'. Many thanks for all you gave me at all stages of my studies.

Now everyone else is wondering when they will be mentioned. Well, I collectively thank all of the hardworking folks who helped do the back-breaking quad riding necessary to collect all the raw data. You are thanked by name in each chapter and are remembered fondly. Fiona Schmiegelow did much of the preliminary ground work and negotiations to actually make the experimental township a reality and made excellent stuffed zucchini in our cabin. Cindy McCallum is the cheeriest and most devoted technician I have ever seen. Seek her out if you ever need a favour!

Nearly last, but not least, is the group of ecology students and professors that keep life interesting, especially at Tuesday-nighters. I think the group substantially increased my learning. There isn't enough room to mention all of the people who individually made my time at university very enjoyable.

My final thank-you is extended to Hilary Jones. Able to offer good advice at critical times, able to become my closest friend and more, and able to cope with my never ending bugging; Thanks.

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Chapter 1

Thesis Introduction

1.0 Research Overview

Throughout North America, fragmented landscapes are becoming increasingly common as a consequence of forest harvesting and agricultural practices, petroleum exploration and transportation developments. Many populations of North American forest-dwelling songbirds, particularly those wintering in the Neotropics, are declining in various parts of their ranges (Robbins et al. 1989, see review in Askins 1993). The declines are probably the combined result of habitat destruction and fragmentation effects on breeding and wintering grounds and of migratory stop-over habitat (Moore and Simons 1992, Terborgh 1992, Böhning-Gaese et al. 1993, Rappole and McDonald 1994).

Fragmentation effects include both physical changes to the habitat and changed ecological processes in the disturbed habitat. The most basic physical alteration affecting birds is a decrease in area, dramatic enough to limit resources in the fragment for breeding. Another physical parameter affecting birds is the shape of the fragment and its spatial relationship to other areas of suitable habitat. Certain species avoid placing their breeding territories near edges, so fragments with a high edge:interior ratio may be unused (Wenny et al. 1993). Physical separation from other suitable habitat influences species use; the degree of isolation of fragments has been negatively correlated with the presence of several forest-dwelling species (Lynch and Whigham 1984, van Dorp and Opdam 1987, Askins et al. 1987, Villard et al. 1995).

Changes in the ecological processes resulting from habitat fragmentation are both abiotic and biotic. Changes to the fragment microclimate is one common abiotic change that changes vegetation structure (see Saunders et al. 1991). These outward changes in the habitat may be direct (e.g., increased shrubs) and indirect; Wenny et al. (1993) hypothesized that ovenbirds may avoid edges because dessication there may negatively affect the prey species of ovenbirds. Three of the biotic changes are competitive exclusion of some species, increased nest parasitism and nest predation (parasitism and predation

reviews in Paton 1994, Andren 1995). Competitive exclusion in fragments often causes replacement of species common in the undisturbed forest by species that are more edge-adapted (Wiens 1989). Species diversity in fragments remains similar, but the community changes. The problems of nest parasitism and predation have been especially pervasive. Nearly all the nests of many species in some fragmented landscapes are affected by these two processes (Wilcove 1985), and the incidences of parasitism and predation are positively correlated with the degree of fragmentation of a landscape (Robinson et al. 1995).

Fragmentation effects have particular relevance to the managed forests in northern Alberta. Large-scale, industrial forest harvesting is now occurring in the boreal forests of the province. Harvesting strategies target old forest for initial cutting, and have an overall rotation (time between successive cuts of the same forest) time of approximately 70 years. This may effectively eliminate a large portion of old forest on the landscape and will certainly change its distribution. Buffer strips, uncut areas left along watercourses, will be one of the few permanent preserves of old forest left on the landscape.

Buffer strips are traditionally left to help preserve water quality and protect fisheries (Hornbeck et al. 1986, Belt and O'Laughlin 1994). They may be either true riparian forest (rooted in the watertable), upland forest, or a combination of both, depending on site-specific characteristics like slope or adjacent waterbody type and buffer width. Outside of their traditional role, buffer strips may also provide high quality habitat to bird species that do not inhabit the adjacent, regenerating forest. Moreover, buffer strips may act as movement corridors, providing links between undisturbed habitat.

Many studies have investigated how bird abundance and species richness or diversity varies between forests near watercourses and forests away from watercourses. Most have suggested that abundance and richness is higher in the forests near water than in upland forests (e.g., Stauffer and Best 1980, LaRue et al. 1995). These differences have been attributed to the increased diversity of vegetation structure and species, the presence of the riparian edge, and increased insect abundance for insectivorous species. Some studies (Murray and Stauffer 1995) have not found such a relationship for birds, or have

even identified a negative relationship (McGarigal and McComb 1992) between those parameters and proximity to water.

Width or disturbance of the buffer strips may affect bird communities. Generally, the similarity to the bird community before disturbance or a bird community present in undisturbed forest of similar structure is inversely proportional to forest width (Johnson and Brown 1990, Keller et al. 1993, Darveau et al. 1995). Species found in large tracts of forest are absent from the smaller or more disturbed buffer strips. Songbirds in these linear habitat fragments could be impacted by any or all of the effects discussed above.

Buffer strips or riparian forest may act as movement corridors (see Bennet 1990), however, there are few data to validate that organisms use them in this manner. Some studies have suggested that birds use upland corridors (e.g., Lovejoy et al. 1986, Haas 1995). From a practical standpoint, areas along watercourses already represent natural pathways in the landscape, provide habitat, and could be conserved in managed landscapes for little additional expense. Based on aspects of metapopulation theory, buffer strips could help maintain animal movements between suitable habitat patches.

Metapopulation theory (Levins 1970) provides a framework that describes how corridors may help conserve species. It models populations that have a patchy, dynamic distribution across the landscape and that are linked by dispersal events. The regional distribution of extant metapopulations changes in response to stochastic extinction and recolonization processes; the survival of the regional population depends on a balance of these parameters. Supposedly, corridors can facilitate interpatch movements, especially during dispersal, by providing a similar matrix (to occupied habitat) through which individuals will move. In this manner, they may specifically help patch populations persist by repopulating fragments where a population has become extinct and by supplementing non-viable populations (rescue effect of Brown and Kodrick-Brown [1977]).

Generally then, previous research indicates that buffer strips have both potential strengths and weaknesses as conservation tools. They may be high quality habitat for species that will not be found in regenerating forest and they may act as travel corridors

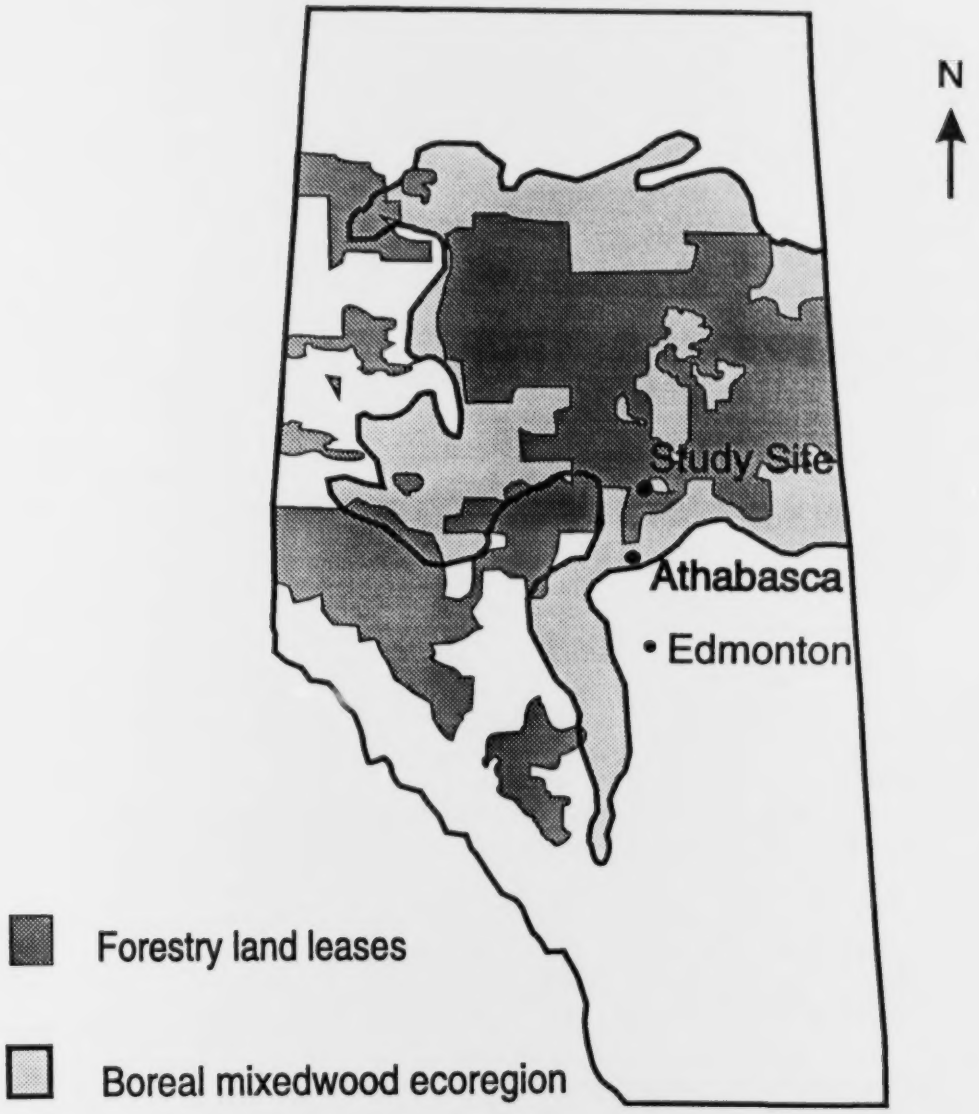

Figure 1-1. Location of the study area in Alberta. Diagram courtesy of S. Cotterill.

between larger areas of forest, but because they will be narrow habitat patches surrounded by a dissimilar matrix, their songbird community may experience fragmentation effects.

In this thesis, I present the results of a research project on buffer strips. I conducted the research near Calling Lake, Alberta (Fig. 1-1). I have two chapters investigating the conservation potential of buffer strips. My research objectives were (1) to evaluate the immediate impact of harvesting on songbird communities in buffer strips and, (2) to determine if buffer strips can support more species at greater abundances than upland forest (both in Chapter 2) and (3) to determine if buffer strips are used as movement corridors by songbirds (Chapter 3). In the last chapter I review my most important results, discuss their significance and provide management recommendations that are based on my research.

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Chapter 2

The Conservation Potential of Riparian Buffer Strips for Boreal Mixedwood Forest Songbirds.[1]

2.0 Introduction

Riparian forests typically contain bird communities that have more species in higher densities than upland forests (Henke and Stone 1979, Stauffer and Best 1980, Décamps et al. 1987, Gates and Giffen 1991, LaRue et al. 1995). This difference has been attributed to the diversity of available habitats at the riparian ecotone (Naiman et al. 1993). In addition to their different habitat structure, riparian areas produce higher numbers of insects (Jackson and Fisher 1986, Gray 1993), potentially increasing the value of riparian habitats for insectivorous birds. In contrast, some studies have reported no overall influence (Murray and Stauffer 1995) or even a negative influence (McGarigal and McComb 1992) of riparian areas on forest bird communities. As in other studies however, these latter two reported significant differences between most vegetation parameters measured between riparian and upland locations. Very few studies have investigated characteristics of avian communities where the vegetation communities have been very similar, leaving only the presence of the edge and waterbody as the difference between upland forest.

Strips of forest that border watercourses are commonly left uncut during timber harvesting, primarily to buffer the effects of forest harvesting on the water quality of adjacent streams or lakes (Hornbeck et al. 1986, Budd et al. 1987, Barling and Moore 1994, Belt and O'Laughlin 1994). The value of some types of buffer strip forest as habitat for songbirds has also been investigated (Johnson and Brown 1990, Keller et al. 1993, Darveau et al. 1995). Generally, adjacent disturbance reduces the number of species that are associated with unbroken forests. Buffer strip width is inversely proportional to the

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1

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similarity of the pre-disturbance songbird community or ones in spatial controls (Stauffer and Best 1980, Keller et al. 1993, Darveau et al. 1995).

Within the last decade in Alberta, three-quarters of the province's 290 000 km^2 of forested land has been placed under management agreements with forestry companies. Harvesting of hardwoods (*Populus* spp.) targets the older stands (>80 years) first and leaves a 100-m wide strip of riparian forest around larger waterbodies (Anon. 1991). These buffer strips are usually dominated by the same vegetation communities as adjacent upland forests, except for a narrow band of true riparian vegetation. Harvesting of all merchantable timber within one area (i.e. a township, 10 × 10 km) is planned on a two or three-pass system, with a minimum of 10 years between passes. As a consequence of this harvesting style and the projected harvest rate (~10 first-pass townships/year), significant areas of forest will be left as buffer strips within an ecologically short period of time (20-40 years). Further, with a projected 70-year rotation, the buffer strips may eventually contain most of the old forest present in the managed landscape. Thus, a measure of their value to songbirds in the boreal mixedwood forest is imperative.

In this paper, I present the results of a two-year study designed to describe the immediate post-harvest effects on songbird communities in buffer strips, and to compare songbird communities in lake-side forest with communities in upland forest. I had two distinct sets of objectives. First, with respect to the harvesting effects, I wanted to determine if creating a buffer strip changed the number of species, or their relative and total abundances, compared to undisturbed lake-side forest. I predicted that species richness would decline in the lake-side forest after adjacent harvesting, as some species would be area-constrained and some would be edge-intolerant. I also predicted that the number of individuals in the community would increase immediately after harvesting, a crowding effect manifested when individuals are displaced from the adjacent cuts into the buffer strips. Second, with respect to the lake-side/upland forest comparison, I wanted to determine how bird communities differed in species composition, richness and relative abundance between lake-side and upland forest. However, I wanted to make this comparison both with and without accounting for vegetation differences. I predicted that

in both instances the communities in lake-side forest would contain more species and individuals than upland forest, as the riparian areas would be higher quality sites.

2.1 Methods

2.1.1 Study Area and Experimental Design

This study was conducted near Calling Lake, Alberta (55°15′ N, 113°35′ W), in the boreal mixedwood forest (Rowe 1972). The study area is dominated by mature trembling aspen (*Populus tremuloides*) and balsam poplar (*P. balsamifera*), with low, but varying densities of white (*Picea glauca)* and black spruce (*P. mariana*). The forests are pyrogenic (Eberhart and Woodard 1987) and range in age from 70 to 140+ years. Understory vegetation is dominated by prickly rose (*Rosa* spp.), lowbush cranberry (*Viburnum edule*) and wild sarsaparilla (*Aralia nudicaulis*) in younger stands, and rose and alder (*Alnus tenuifolia* and *A. crispa*) in older stands. The forest has a high degree of natural patchiness because of minor topographic variation and the historical dominance of fire in the system.

This investigation was part of a large-scale experimental study on forest fragmentation (Schmiegelow and Hannon 1993). All monitoring in year 1 (1993) was in undisturbed habitat and, in year 2 (1994), was after clearcutting of adjacent forests (cut during the winter). The buffer strips in this study typically consisted of 1-5 m of shrubby, wetland vegetation and 90-110 m of forest surrounding lakes. The width of each buffer strip was measured from the high water mark of each lake. Because width is the requisite characteristic of buffer strips and not forest *per se*, a few buffer strips were composed completely of riparian vegetation or a more equal combination of upland and riparian vegetation.

In 1993, 25 lake-side stations were sampled, 11 of which became treatments in 1994 when adjacent forest was cut (now buffer strips), while 14 remained as unharvested controls. Control and treatment stations were interspersed, and all stations were distributed between two different lakes in the study area. Each sample point was ≥200 m from any other, and was placed 50 m from the lake-forest boundary. Treatment points were therefore centred in the buffer strips and control points were 50 m upland from the

lake/forest edge.

I also sampled 99 stations in upland forest in both years. All were in undisturbed forest in 1993, but in 1994, following harvesting, 66 stations were distributed in 18 forest blocks, ranging in size from 1-40 ha (see Schmiegelow and Hannon 1993 for design details, and Schmiegelow et al. in review for results). The other 33 stations remained in undisturbed forest as upland controls. All upland stations were ≥150 m (but up to several km) from the nearest riparian edge and, within a block, were each separated by 180-200 m. The distance to the nearest harvested edge was slightly greater for upland treatments (50-100 m) than for the lake-side treatments (50 m).

2.1.2 Data Collection

Estimates of bird species richness and relative abundance were collected using point counts (Ralph et al. 1993) at each survey station. Counts were conducted 5 times during the breeding season (late May to the end of June) in both years. Multiple observers were used and rotated among all stations. Visits to census points were distributed throughout the period from sunrise to 1000 hrs. Each count lasted 5 min. and only birds recorded within 50 m were included in analyses. Each year, the first round of counts was conducted before birds had completely settled into breeding territories. The data from this round were excluded from all analyses except for the bootstrapped estimates of richness (see below).

To record finer-scale data on changes in species abundance and distribution caused by adjacent harvesting, songbird territories were spot-mapped (Bibby et al. 1992) in 3 strips of lake-side forest in 1993. In 1994, two of the areas became buffer strips (treatments) and one remained in undisturbed forest as a control. All spot-mapping grids were 100 m wide (width of the buffer strips). The treatment buffer strips were 700 and 800 m long, while the control strip was 700 m long. The control strip had over 100 ha of undisturbed upland forest adjacent to it (Fig. 2-1A). Treatment buffer #1 (Fig. 2-1A) had 200 m of adjacent clearcut, but treatment buffer #2 (Fig. 2-1B) was separated from a 10 ha forest reserve by 30 m along 45% of its length. Each area was visited 8 times during

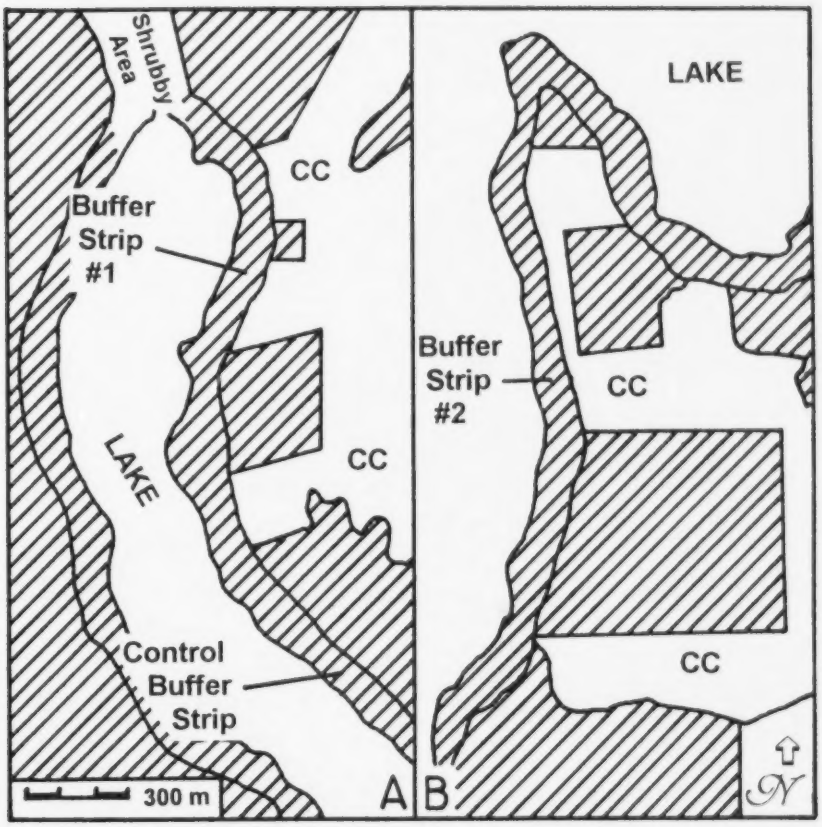

Figure 2-1. Diagrams of buffer strips #1, #2, and the control buffer strip that were all spot-mapped in both years. All of the cross-hatched area is forest and the unshaded areas labelled 'CC' are clearcuts.

late-May and June. The minimum requirement for delineating a territory was 2 registrations of a singing male, separated by at least 10 days (Bibby et al. 1992) or confirmed evidence of breeding (nest, broods, etc.).

Vegetation data were collected at all stations based on a modified version of the protocol of Martin (1992). Four 0.04 ha vegetation plots were surveyed at each point count station. One was centered on the station, and the other 3 were centered 40 m away at 0°, 120° and 240°. The following data were collected: estimated ground cover (nearest 5%) of 6 broad vegetation classes in four 1-m^2 quadrats per plot (forb, shrub, moss, grass, leaf litter, all green [plant] cover); depth of leaf litter (average of 4 measures per plot); number of stems of shrubs by species in five-1 m^2 quadrats; number of saplings (<2.5 cm diameter at breast height [dbh]) and poles (2.5 cm < dbh < 8 cm) by species in 0.008 ha sub-plots; number of trees in 4 dbh classes (8-15, 15-23, 23-38, >38 cm) by species; number of snags <12 cm dbh; number, dbh and height of snags >12 cm dbh; canopy height and cover (measured with a densiometer); and subcanopy and tall shrub layer height.

2.1.3 Data Analyses

2.1.3.1 Harvesting Effects

Effects of harvesting on species richness and abundance were tested using repeated measures ANOVA. Because I had only two groups and two times, the treatment × time effect of the RM-ANOVA was equivalent to *t*-tests of a treatment effect on the between-year mean differences (profile analysis, von Ende 1993). I used the Jaccard coefficient to compute species turnover between years. It divides the number of species in common by the total number of species observed at a station. It varies between 1 and 0; when J = 1, the stations had all the same species in both years and none in common when J = 0. Percent species turnover was therefore defined as (1 - J) × 100. Calculation of J was not confounded by comparing the same station between years because all comparisons were within-station, so any correlation effect was equivalent across groups.

2.1.3.2 Lake-side/Upland Forest Comparison

I used cluster analysis to quantify species co-occurrence patterns (i.e. form associative bird communities). Total abundance of each species at each station was

calculated using both years of survey data. Hogstad (1993) found that turnover in a relatively large (1 km^2) area of boreal forest was approximately 15%. I therefore used both years of data collectively to determine presence and abundance at each station to compensate for the highly variable presence of species on my small plots. The number of males at a station was computed as the maximum number of males per species detected on any one survey round per year. The resulting matrix was clustered using the Phi-Square measure for count data (corrects for frequency of observation) and Ward's method of hierarchical cluster analysis (Ward 1963, see below).

Species richness between communities is best compared by using the total number of species observed. However, for this comparison to be valid, the number of individuals in each community must be equal (Ludwig and Reynolds 1988). Species richness at upland stations was estimated using bootstrapping because there were more upland than lake-side stations sampled. The bootstrapped sample contained the same number of observations per survey round as the lake-side forest, which satisfied the constraint that richness is a function of the number of individuals surveyed. The primary assumption of bootstrapping is independence of observations (Dixon 1993), so only one census round was compared at a time. However, the best independent estimate of number of unique species observed at any one station per census round was from both years of data, so counts were pooled across years, making 5 (all census rounds included) comparable estimates. I iteratively subsampled, with replacement, 150 times from the larger upland dataset, counting the number of unique species on each iteration. A mean estimate of species richness with 95% confidence intervals was calculated from the new dataset.

The vegetation dataset contained >100 variables when species were considered individually. To reduce the number of variables to be considered, I chose a subset of descriptive and summary variables that would represent the structure and broad vegetative distinctions that occurred between stations, adopting a structural, rather than floristic, approach (e.g., Smith and Shugart 1987). I constructed two-dimensional principal component factor plots for each of the ground cover, tree and shrub data sets to aid in selecting the subset. None of the PCAs produced meaningful components (broken stick

criteria, Legendre and Legendre 1983, Jackson 1993), so no summary variables were derived by this method. Instead, I used the factor plots either as guidelines to select a subset of the original variables that polarized the data or I interpreted the gradients that the plots revealed (e.g., deciduous - coniferous) and created summary variables that would represent them.

Twenty-one variables were used for analysis of vegetation structure. Five percent-cover variables (forbs, grass, shrubs, leaf litter, and moss) and four physical descriptors (canopy, sub-canopy and tall shrub layer height, and canopy closure) were kept without modification. I summarized my tree data set into five variables (total number of deciduous stems, mesic conifer stems (white spruce, jack pine *Pinus banksiana*, and balsam fir *Abies balsamea*), hygric conifer stems (black spruce, larch *Larix laricina*), total deciduous basal area, and total coniferous basal area). I included poles as the smallest and fifth size class of trees and summarized the sapling data into two variables (total coniferous and total deciduous saplings). The shrub data set was reduced to a single variable, total stem density. Finally, I summarized the snag data into four variables (number of snags <12 cm dbh; number >12 cm dbh, their average height and total basal area). Other variables were not included.

To control for vegetation variation when making the bird community comparisons, I needed to select a sub-group of stations that was similar. I used cluster analysis and MANOVA to define a subgroup of similar stations from the 91 stations that had vegetation data (25 lake-side and 66 upland). The cluster analysis was used to provide a sample within which I could test the hypothesis that the vegetation communities were similar.

Before clustering, each vegetation/structure variable was standardized to a maximum of one. Between station dissimilarity was calculated by the squared Euclidean measure, and stations were clustered using Ward's method. Ward's method builds clusters out of the combination of groups which minimizes the new cluster's within-group variance, and is considered the optimal hierarchical clustering technique (Kent and Coker 1992).

Four distinct clusters were formed in the analysis. One contained a nearly equal

number of upland and lake-side stations, that were then compared with a multivariate ANOVA. Variables with markedly non-normal distributions were $\log(x + 1)$ transformed to satisfy test assumptions (Maxwell and Delaney 1990). Pillai's trace was used to calculate an F-ratio, as it is the most robust to violations of assumptions (Norušis 1993).

A *t*-test was used to test univariate between-group differences, unless assumptions were violated. In these cases, a Mann-Whitney *U* test was used. I used the paired versions of the above tests to compare between-year differences of stations.

Refer to Appendix 1 for scientific names of all bird species.

2.2 Results

2.2.1 Effects of Adjacent Harvesting

Species richness and total abundance were not affected by harvesting (Table 2-1). The control stations had significantly fewer individuals than treatment stations in 1994 ($t = 2.19$, $p = 0.039$). The decrease in the controls was paralleled by a nonsignificant (paired-$t = 0.72$, $p = 0.47$) 7.2% decline in average abundance at upland control stations.

Species turnover also did not differ between treatments and controls (control $\bar{x} =$ 77.2%, isolates $\bar{x} = 70.2\%$, $t = 1.59$, $p = 0.125$). These turnover rates were not significantly higher than in large tracts of undisturbed upland forest ($n = 33$ upland control stations, $\bar{x} = 68.7\%$, $n = 25$ lake-side stations, $\bar{x} = 74.2\%$; $t = -1.25$, $p = 0.217$).

Table 2-1. Per station means of the number of individual species and total abundance of songbirds in lake-side forest. No stations had adjacent cutblocks in 1993, while 'treatment' stations did in 1994.

Station Type	*n*	*Number of Species*		*Treatment Effect*[1]	*Total Abundance*[2]		*Treatment Effect*
		1993	*1994*		*1993*	*1994*	
Treatment	11	9.45	9.64	$F = 2.42$	10.36	10.36	$F = 2.13$
Control	14	9.29	7.64	$p = 0.133$	9.61	7.79	$p = 0.158$

[1] *Treatment effect is the year × treatment interaction term of a repeated measures ANOVA.*
[2] *Total abundance is the mean of the per-station totals.*

Changes in bird abundance after creation of the buffer strips were not dramatic.

Based on spot-mapping data, the number of territories in all 3 buffer strips increased between years (Table 2-2). The overall differences per species were nonsignificant in all 3 strips (Wilcoxon Matched-Pairs Rank-Sum test, $Z \geq -1.481$, $p \geq 0.139$) because the relative abundance of some species increased while others decreased. In the control and #2 treatment buffer, 7 species increased and 2 decreased (Table 2-2). Ten species declined and 9 species increased in the #1 treatment buffer.

Only a few changes in territories were consistent between the spot-mapped areas. In both treatments, 3 species either disappeared or dropped in relative abundance (ovenbird, Philadelphia vireo, rose-breasted grosbeak), while one species increased (red-eyed vireo) (Table 2-2). In the control, the number of territories of ovenbirds increased and the number of red-eyed vireos remained stable (the other two species were not recorded in the control). The point-count data only supported the spot-mapping trends for one species, the ovenbird. It was negatively affected by harvesting (contrast of treatment vs control; $U = 38.0$, $p = 0.019$).

2.2.2 Lake-side/Upland Forest Comparison

I checked for a harvesting effect on upland plots before any comparisons were made between lake-side and upland forest. No treatment effect (year × treatment term) was observed for either species richness ($F = 0.01$, $p = 0.925$) or for species abundance ($F = 0.05$, $p = 0.830$). Both years of data were therefore pooled for each location.

2.2.2.1 Bird Community Structure

Four communities were identified by cluster analysis (Fig. 2-2). The community labelled as 'group 4' contained 13 species that, except for 2, had significantly higher abundances in lake-side forests compared to upland forest (Bonferroni adjusted $\alpha = 0.004$; Mann-Whitney U tests, all $p \leq 0.0044$ except orange-crowned warbler, $U = 750.0$, $p = 0.09$; house wren, $U = 759.5$, $p = 0.26$). The ruby-crowned kinglet was the only species that was significantly more abundant ($U = 640.0$, $p = 0.004$) in lake-side forests that was not in this cluster. The brown-headed cowbird was excluded from the cluster analysis because it is not territorial, but this species did show significantly higher abundances in the lake-side forest ($U = 394.5$, $p < 0.001$).

Table 2-2. Numbers of territories of each species at three buffer strips in 1993 and 1994 based on spot mapping. The control buffer had no adjacent harvesting, while the two treatment buffers did. Half territories were counted when there were registrations inside and outside the plot for (presumed) one individual. Only 5 of 25 point count stations overlapped with these spot-mapped areas.

Species	*Control Buffer*		*Treatment Buffer #1*		*Treatment Buffer #2*	
	1993	*1994*	*1993*	*1994*	*1993*	*1994*
yellow-bellied sapsucker	0.0	2.0	1.0	0.0	2.0	2.0
least flycatcher	0.0	1.0	16.5	15.0	6.5	9.5
western wood-pewee			0.0	1.0	0.0	1.0
black-capped chickadee					0.0	1.0
house wren			1.0	1.0		
red-breasted nuthatch			0.0	1.0		
American robin			1.5	2.0	1.0	1.0
cedar waxwing			0.0	2.0		
red-eyed vireo	2.5	2.0	2.0	5.0	0.5	5.0
Philadelphia vireo			1.0	0.0	1.0	0.0
yellow-rumped warbler	3.5	4.0	4.5	4.0	3.0	3.0
yellow warbler			5.5	6.5	3.0	3.0
mourning warbler			3.5	3.0	1.0	1.0
Connecticut warbler	0.0	1.0			0.0	1.0
Canada warbler			1.0	1.0		
ovenbird	2.5	4.0	1.5	0.0	4.0	1.5
American redstart			1.0	0.0		
rose-breasted grosbeak			1.0	0.0	2.0	0.0
song sparrow			3.0	4.0		
chipping sparrow	1.0	2.0	1.0	1.0	0.0	2.0
white-throated sparrow	1.0	2.0	3.5	5.0	3.0	3.0
Lincoln's sparrow	2.0	0.0	1.0	1.0	1.0	4.0
swamp sparrow			1.0	0.0	2.0	2.0
northern oriole			1.0	0.0		
red-winged blackbird			0.0	1.0	2.0	2.0
western tanager			1.0	1.0	1.0	1.0
Area	7 ha		8 ha		7 ha	
Totals	12.5	18.0	52.5	54.5	33.0	43.0
Number of Species	6	8	20	17	15	17

The 3 other communities contained birds which either had a significant preference for upland stations (Bonferroni adjusted α used for each community; American redstart, black-throated green warbler, and white-throated sparrow; all $p \leq 0.003$) or no

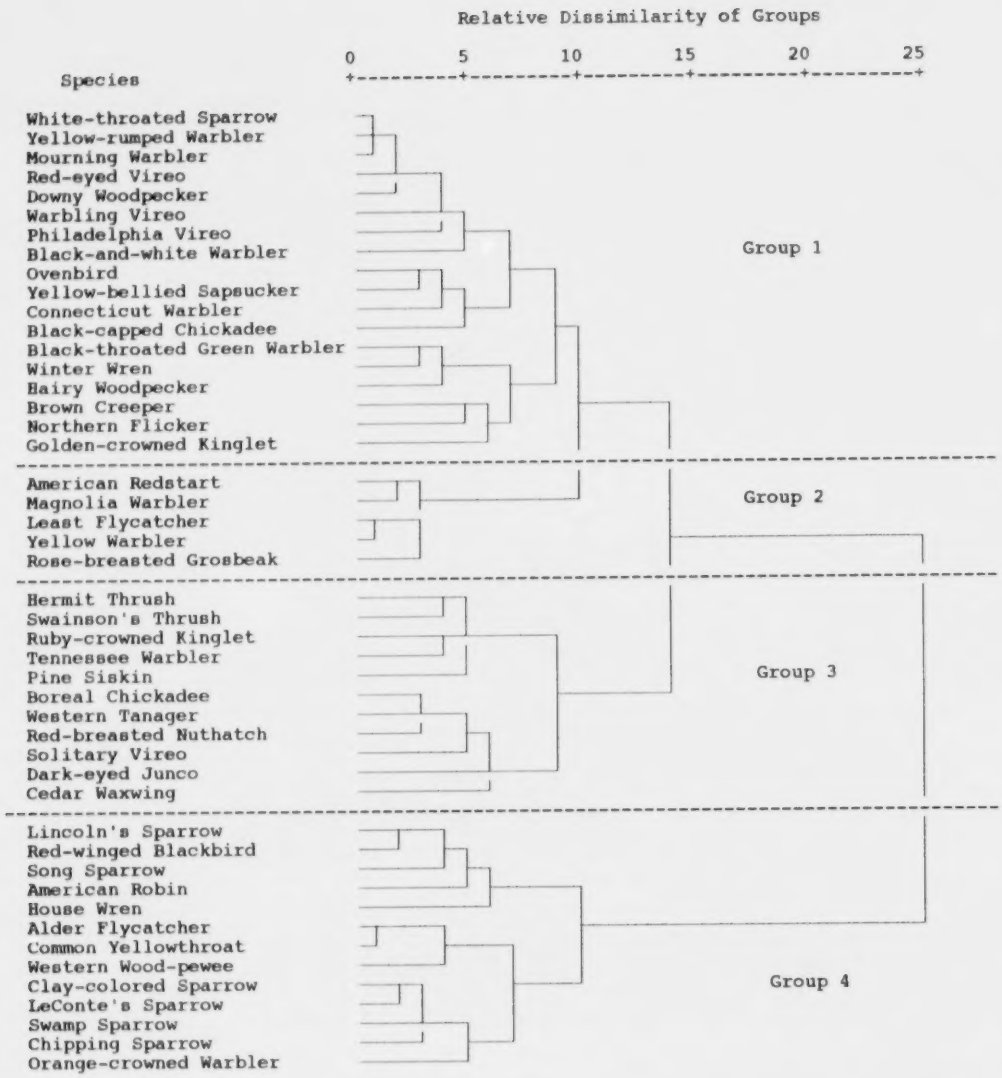

Figure 2-2. Dendrogram of bird communities produced by cluster analysis on inter-species associations. Based on a combination of habitat preferences in Ehrlich et al. (1988) and personal observation, the groups could be subjectively labelled as: Deciduous/mixed generalists, with some species associated with old white spruce (Group 1), old deciduous-preferring (Group 2), higher coniferous preference (Group 3), and riparian/open habitat preference (Group 4).

preference. Although a sequential Bonferroni adjustment (Rice 1989) would have been less conservative, test results were either highly significant or clearly not significant, so the conservative measure was used. The station preference comparisons do not account for any vegetation differences (see analyses below), so higher average abundances may reflect differences in suitable habitat, not only the presence of the riparian edge and habitat.

2.2.2.2 Bird Community Comparisons

The number of species in lake-side forest was significantly higher (exceeded the 95% confidence intervals) than at upland stations, without controlling for vegetation differences (Table 2-3, top). On average there were 25.8% more species at lake-side stations. There were also significantly more individuals (24.7%) per station in lake-side forest (lake-side $\bar{x} = 9.43$, upland $\bar{x} = 7.56$, $U = 539.0$, $p = 0.01$). Abundance did not differ significantly between years at the lake-side stations or upland stations (paired-$t \geq 1.57$, $p \geq 0.120$).

Four groups were defined by the cluster analysis of survey stations based on the 21 parameters describing their vegetation communities (Fig. 2-3). The habitat designations are based on some univariate differences between clusters. The cluster that contained nearly equal proportions of upland ($n = 14$) and buffer ($n = 11$) stations was dominated by aspen, but had the highest coniferous content of the four. The vegetation parameters of lake-side and upland stations within this cluster did not differ significantly (MANOVA, Pillai's $F = 1.64$, $p = 0.384$). The power of this test was low (0.18) with all variables. The MANOVA was still nonsignificant ($p = 0.108$, power = 0.61) when 7 variables with unequal variances were removed from the analysis. One of 21 variables, average height of the tall shrub layer was significantly different using univariate (Mann-Whitney U) tests and a Bonferroni adjusted α ($p \leq 0.002$), while two others (average canopy height [$p = 0.003$], average forb cover [$p = 0.006$]) were significant if a less conservative $\alpha = 0.01$ was used (5 test adjustment).

The only major difference between upland and lake-side stations was the presence or absence of the edge between the forest and the waterbody or shrub zone within the vegetatively similar subgroup. Bird species richness was still, on average, higher at the

Table 2-3. Comparison of species richness at lake-side stations (n = 25) and upland stations (n = 66) during each of 5 point count surveys. Estimates made without controlling for vegetation differences were always extracted out of the larger, upland sample by bootstrapping. Estimates after controlling for vegetation differences (lower section) were made by subsampling individuals out of the larger of the two data sets, on a per survey round basis. Confidence intervals only appear for the bootstrapped estimate of richness. The independent sampling unit used to count unique species was the number of detections.

Count Number	*Estimated Number of Species (95% C.I.)* *Lake-side Sites*	*Upland Sites*	*Percent more in Lake-side Sites*
	Not controlling for vegetation differences		
1	41	33.7 (33.4-34.0)	+21.7%
2	38	30.1 (29.8-30.5)	+26.2%
3	38	32.1 (31.7-32.4)	+18.4%
4	38	27.5 (27.3-27.8)	+38.2%
5	42	33.7 (33.4-34.0)	+24.6%
		Net Difference	**+25.8%**
	Controlling for vegetation differences		
1	20.6 (20.5-20.8)	25	- 21.3%
2	28	19	+47.4%
3	25.4 (25.3-25.5)	21	+21.0%
4	23	20.2 (20.1-20.3)	+13.9%
5	22.7 (22.6-22.8)	25	- 10.1%
		Net Difference	**+10.2%**

lake-side stations (Table 2-3, bottom), though not as consistently as for comparisons made irrespective of vegetation differences. Average abundance was also significantly higher (38.2%) in the lake-side forest (lake-side $\bar{x} = 8.00$, upland $\bar{x} = 5.79$, $U = 32.0$, $p = 0.01$). Again, the average abundance per station was compared between years (before pooling) and did not vary significantly at either lake-side or upland locations (paired-$t \geq 1.64$, $p \geq 0.125$).

There were 5 species unique to lake-side forest (alder flycatcher, Lincoln's sparrow, song sparrow, swamp sparrow, red-winged blackbird) and 1 species unique to upland stations (winter wren) within the subgroup of similar stations. Species unique to the lake-side stations are all common to riparian habitat (*pers. obs.*, Ehrlich et al. 1988).

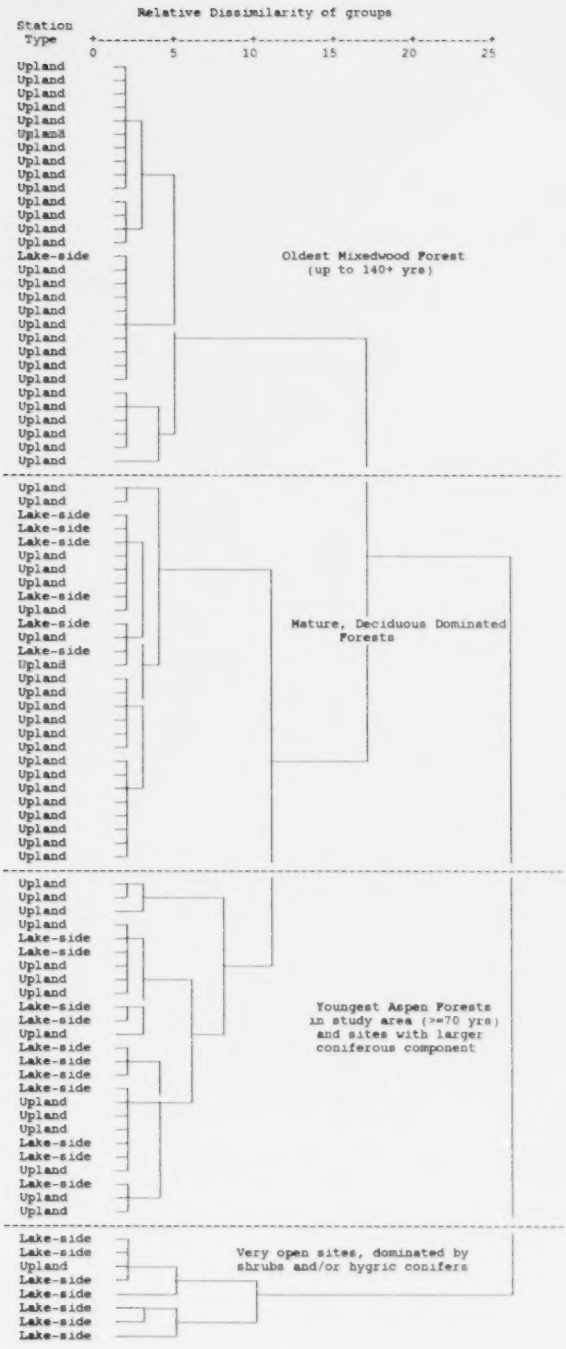

Figure 2-3. Dendrogram of vegetation communities. Ages are approximate and are derived from recent vegetation inventory maps. The group labels are descriptions based on some observed univariate differences among the groups.

However, mist netting evidence (Machtans, unpubl. data) from the buffer strips that were spot-mapped (Fig. 2-1) indicated that the three sparrow species also use the forest away from the lake edge. Each species was captured at least once ≥70 m from the riparian/forest interface. Red-winged blackbirds were captured 25 m upland from the interface, but no alder flycatchers were captured.

Twenty-two species were present in both lake-side and upland forest stations, and present at ≥ 3 stations of either one. I used this criterion to compare species abundances between the two locations. Of these, solitary vireos were significantly more abundant at upland stations ($U = 45.0$, $p = 0.04$) and brown-headed cowbirds ($U = 39.0$, $p = 0.02$), western tanagers ($U = 36.0$, $p = 0.01$) and yellow warblers ($U = 46.0$, $p = 0.05$) were significantly more abundant at lake-side stations. For the above tests, observed significance levels were too high to use the sequential Bonferroni adjustment and the standard adjustment ($\alpha = 0.05/22 = 0.002$) would have produced unacceptably high Type II errors for my sample size.

2.3 Discussion

2.3.1 Effects of Adjacent Harvesting

My prediction that species richness would decline after adjacent harvesting was not supported. Clearcutting of adjacent forests had no immediate (first year post-harvest) effect on species richness. The prediction was based on the hypothesis that the buffer strips would have species adapted to edge habitats on the riparian side of the forest, and that these species would persist after harvesting while the number of species present because of neighboring, extensive upland forest would decrease. If some clearcut-edge preferring species invaded the disturbed areas after harvest (as in forest fragments, e.g., Lynch and Whigham 1984), the turnover rate at disturbed stations should have been higher. Post-fragmentation communities often have similar diversity to pre-fragmentation communities, but are prone to species replacement. Forest-interior species are often replaced by species that are more edge-adapted (Wiens 1989). It was unexpected that turnover rates would not differ, but was in agreement with the other data that showed no harvesting effect. Overall, the high turnover rates (*ca.* 70%) calculated are a result of

analyses at the station level. Pooling within treatments decreased the annual turnover rate (35% treatments, 44% controls), but still maintained proportional differences. Harvesting effects may still occur, but may take years to become detectable.

My prediction that abundance would increase in buffer strips, relative to control lake-side forest, was not supported. Abundance did not change significantly in response to treatment. There was no decline in abundance at the lake-side treatment stations, but there were slight declines at lake-side and upland control stations. This suggests that slight post-harvest crowding occurred (Whitcomb et al. 1991, Bierregaard and Lovejoy 1988, Darveau et al. 1995). This effect was neither statistically or biologically significant; the between-year similarity of the treatments implies that resources would not be limiting to the songbirds.

The only consistent result from point-count surveys and spot-mapping data was the negative effect of adjacent harvesting on ovenbirds. Before harvesting of the forest adjacent to the #1 treatment buffer, several ovenbird territories extended into the lake-side forest from the upland forest, as well as 2 that were contained within the strip (Table 2-2). Following harvesting, the single remaining pair using the buffer had its territory at the widest point of the buffer, where a 1 ha reserve was attached. This type of response was also documented by MacClintock et al. (1977) for a pair of ovenbirds using a linear strip of habitat.

Ovenbirds are known to be sensitive to fragmentation in eastern North America (Whitcomb et al. 1981, Robbins et al. 1989). In my study, the pair was observed using over 5 ha of the buffer, whereas ovenbird territories in undisturbed forest in both years were never larger than 2 ha (Machtans, unpublished data). In all mapped buffer strips, ovenbirds tended to locate their territories in the portion of the strip away from the riparian edge. Similarly, LaRue et al. (1995) found that ovenbirds were more abundant away from riparian edges and MacClintock et al. (1977), Kroodsma (1984), and Wenny et al. (1993) found that ovenbirds generally avoid edges. These results suggest that 100-m wide buffer strips are likely not suitable for ovenbirds, in agreement with Stauffer and Best (1980) who reported that ovenbirds did not breed in riparian strips <175 m wide.

The only other non-trivial result from spot mapping was the increased abundance of red-eyed vireos in the treatments. This suggests that adjacent harvesting did not deter red-eyed vireos from using the buffer strips (not negating the results of Van Horne 1983). Again, my data are in agreement with Stauffer and Best (1980), who found red-eyed vireos in buffer strips <100 m wide.

2.3.2 Are There Different Communities in Lake-side Forest?

The forests that border watercourses have some different bird species when compared to upland forest, those typically associated with a riparian ecotone (Ehrlich et al. 1988). Other bird species associated with lake-side forest were found in equal abundance in either upland or buffer stations except for the 3 species that were more abundant at the upland stations. The clustering of vegetation communities identified some distinct separations among forest types in the study area. Though all the upland forest I studied was dominated by *Populus* spp., there was a tendency for the stations in lake-side forest (locations of the buffers) to cluster into a group that was younger and contained more coniferous trees.

2.3.3 Species Richness and Abundance Between Upland and Lake-side Forest

My prediction that songbird species richness and relative abundance would be higher in lake-side than upland forest was supported. Before accounting for vegetation differences, the number of unique species and number of individuals was ~25% greater in lake-side forest. My results support the notion that bird communities in forests at or near riparian ecotones are richer and relative abundance is higher than at upland sites, similar to most other studies conducted in riparian woodlands (e.g., Stauffer and Best 1980, Emmerich and Vohs 1982, Décamps et al. 1987, Gates and Giffen 1991, LaRue et al. 1995).

My prediction that lake-side and upland forests with statistically similar vegetation communities would support more species and individuals was also supported, similar to findings in coniferous forest (LaRue et al. 1995). Equal-sized areas of lake-side forest supported ~10% more species and ~38% more individuals than upland patches. This difference was not just due to the additional species directly associated with the riparian

edge; without including the 5 species unique to lake-side forests, average abundance was still 14% higher than upland stations. Two other studies (McGarigal and McComb 1992, Murray and Stauffer 1995) that reported an opposite (or no) effect both reported significant differences in over 50% of vegetation parameters between upland and riparian areas.

LaRue et al. (1995) discussed the positive effect of the riparian edge in terms of various attributes of increased vegetation density, diversity, and structure. A logical outcome of these characteristics is also a change in the type of insect community that would be present, potentially diversifying the food resources of insectivorous songbirds. Riparian areas also produce more insects than upland areas (Jackson and Fisher 1986, Gray 1993). Songbird species may have smaller territory requirements if resources are more abundant (Smith and Shugart 1987 and references therein), accounting for the higher observed relative abundance. From a resource standpoint, lake-side forest may be much more valuable to avian communities than similar upland forest.

Comparisons at the species level only partially supported my second prediction that species present at both upland and lake-side stations would reach higher abundances in lake-side forest. Of the 3 species that had higher abundance in lake-side forest (in the subset of vegetatively similar stations) the brown-headed cowbird is the most interesting. This species also had significantly higher abundance there when vegetation differences were not accounted for (see discussion below). Gates and Giffen (1991) also found that riparian areas supported the highest abundances of cowbirds in a primarily forested landscape. Assuming higher cowbird abundance leads to more parasitism, species using lake-side forests may be experiencing higher levels of nest parasitism than those using upland forests.

2.4 Conservation Potential of Riparian Buffer Strips

The conservation potential of riparian buffer strips for songbirds is limited for several reasons. First, buffer strips that are 100 m wide will likely be unsuitable for certain species. Effects of adjacent harvesting were detectable for some species within the first year after harvesting. Longer-term studies (Darveau et al. 1995) have shown that bird

communities may take several years to adjust to the changes imposed by harvesting and effects could become more pronounced or affect more species in the future. Using productivity data would be the most prudent way to assess those effects. Expecting the old forest left as buffer strips to support the communities found in upland forest may not be realistic for certain species (e.g., solitary vireo and ovenbird) unless width could be increased to accommodate species affected by the proximity of an edge (natural or anthropogenic).

Second, the high relative abundances of cowbirds recorded in buffer strips are a concern. Currently, the incidence of cowbird parasitism on one warbler species (American redstart) in the study area is extremely low (M.-A. Villard and S.J. Hannon, unpublished data) and the regional landscape is still relatively unfragmented. But, in 20 or 30 years when buffer strips account for significant portions of old mixedwood forest in the landscape, the increased parasitism pressures on individuals then restricted to buffer strips could significantly affect reproductive success. One important limitation for cowbirds is that deciduous clearcuts regenerate very rapidly (up to >1 m/yr initially), so the openings created by harvesting may not be suitable to support temporary influxes and increase the current rates of parasitism.

Finally, buffer strips may become susceptible to fire in the future, as they remain unharvested (and current fire suppression disrupts the historical fire regime). In my study area, the lake-side forest presently appears to be no older than the oldest upland forest (Fig. 2-3, group 1), indicating lake-side forest burns at least as often as upland forest. The linear remnants will age and become increasingly prone to ignition as fuel loads increase. Any fire burning through a buffer strip would have a distinct and continuous path of forest (with high fuel loads) to follow. The chances of losing large portions of the remaining old forest (the buffers) might increase over time with the combination of these two factors.

In summary, riparian buffer strips have limited value as reserves of older forest for songbird communities. Forests near watercourses *do* support rich and dense songbird communities, but the issue of appropriate buffer strip width must be resolved. The relative abundance of cowbirds and the probability that buffer strips might eventually become fire

prone could be serious long-term problems. A useful solution would be to have larger reserves of forest adjacent to watercourses. The issue of unnaturally old forests and susceptibility to fire might be dealt with by a system of reserves that are harvested on longer rotation, such as discussed by Harris (1984).

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Chapter 3

Use of Riparian Buffer Strips as Movement Corridors by Forest Birds[2].

3.0 Introduction

The ability of reserve-connecting corridors to retain or restore biodiversity in fragmented landscapes has elicited considerable debate (Simberloff & Cox 1987; Noss 1987; Hobbs 1992; Simberloff et al. 1992; Hess 1994), but few empirical studies supporting either side. The potential advantages of corridors include facilitating movements to and from reserves, providing additional habitat for individuals in reserves, and providing cover from predators during movement (see Noss 1987 for details). Negative aspects of corridors include the loss of alleles to drift in a large number of refuges, an increased risk of propagation of catastrophes such as fire, introduced species, or contagion (Hess 1994), and an increased risk of predation on dispersing individuals by edge-inhabiting predators (Noss 1987; Simberloff et al. 1992). In agreement with Noss (1987), I believe that some critiques of the value of corridors in recently fragmented landscapes argue moot points; pre-settlement landscapes were generally characterized either by continuous habitat or by mosaics of habitat with a high degree of connectivity (*sensu* Merriam 1991).

A variety of studies on different species have shown that corridors have conservation benefits (for reviews, see Bennett 1990 and Saunders & Hobbs 1991). Greater persistence of species in patches connected by similar habitat has been demonstrated several times, although this was not direct evidence of corridor use *per se* (MacClintock et al. 1977; Lovejoy et al. 1986; Saunders 1990). Further, corridor use has been observed for some mammal species, including cougar (*Felis concolor*) (Beier 1993) and several species of rodents (Henderson et al. 1985; Merriam & Lanoue 1990; La Polla & Barrett 1993). However, research demonstrating how or whether birds use corridors is

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A version of this chapter has been accepted for publication (December 4, 1995). The only changes are in pronoun use, some formatting details and the absence of an abstract. Machtans, C.S., M.-A. Villard, and S.J. Hannon. In press. Use of riparian buffer strips as movement corridors by forest birds. Conservation Biology.

very scarce. Wegner and Merriam (1979) and Johnson and Adkisson (1985) reported that birds moved more often along fencerows than directly across open areas between forest patches. Dmowski and Kozakiewicz (1990) found that birds used a shrubby corridor more frequently to access riparian areas than a more open route. Haas (1995) found that movements of adults of three bird species were significantly more frequent between sites connected by wooded corridors than between sites not connected. Only the last study observed patterns of occupancy resulting from observations of dispersal events.

It seems counter-intuitive that organisms as vagile as birds would need corridors to persist in a fragmented landscape. However, several authors have suggested that the open space between forest fragments may form a barrier to songbird movement (Whitcomb et al. 1981; Lynch and Whigham 1984; Lens and Dhondt 1994). Evidence supporting the existence of such barrier effects includes the observation of isolation effects on the patterns of occupancy of some forest bird species in forest patches (Whitcomb et al. 1981; Lynch and Whigham 1984; Askins et al. 1987; van Dorp and Opdam 1987; Robbins et al. 1989; Villard et al. 1995).

To my knowledge, no empirical study has shown whether isolation or barrier effects can be reduced by juvenile dispersal through corridors. Integrating the results of several investigations does suggest that this may be the case. Lens and Dhondt (1994) found that juvenile immigration and emigration into and out of habitat fragments were delayed relative to continuous forest. This suggests that juveniles have a behavioral reluctance to cross open areas, indicating a specific life-history stage when the open spaces are perceived as barriers. In addition, Morton (1992) found that juveniles of a migratory species of sparrow (*Zonotrichia leucophrys*) have an extensive post-fledging dispersal period before migration. If juveniles select their breeding territories shortly before fall migration, as suggested by Brewer and Harrison 1975, Adams and Brewer 1981, Morton et al. 1991, and Morton 1992, then unimpeded natal dispersal (*sensu* Greenwood & Harvey 1982) is critical to metapopulation dynamics. Therefore, the link between isolation effects and population demography may be tied to the reluctance of juveniles to cross open spaces and corridors may reduce these effects.

In boreal Alberta, the forested landscape is relatively continuous. The most prevalent disturbance is the extensive and intricate patchwork of seismic exploration lines (cutlines). However, in the last decade, three-quarters of the province's 290 000 km^2 of forested land has been allocated under management agreements to forestry companies. Harvesting operations utilizing hardwoods (*Populus* spp.) are targeting old stands (>100 years) first, and have a short-rotation schedule (*ca.* 70 years). This intensive management will rapidly fragment the forest, especially the oldest age classes. Buffer strips are currently left after cutting, and will comprise a significant portion of older forest left uncut on the managed landscape. The creation of corridors can be prohibitively expensive (a major criticism of Simberloff et al. 1992), however, in a harvesting context, they can be integrated into management plans with minimal expense and planning. I still do not know whether and to what extent corridors would maintain or enhance movements and therefore would be useful as a conservation strategy.

In this paper, I present the results of a three-year field experiment addressing the use of riparian buffer strips as movement corridors by songbirds between forest fragments created by clearcut harvesting of adjacent areas. Part of my experiment had a before-and-after harvest component (see Schmiegelow and Hannon 1993), so I generated predictions based on comparisons between temporal controls and treatments (the same site before and after treatment), and between treatments and spatial controls (separate sites monitored simultaneously), accounting for differences in songbird abundance. I predicted that (1) after harvesting of adjacent forest, the number of captures would increase in areas that were left as riparian buffer strips as birds move preferentially through the buffer strip instead of crossing the clearcut. I also predicted that (2) the number of captures would be higher in buffer strips than in spatial controls for the same reason, and that (3) the number of forest birds seen moving across open areas between fragments would be lower than the number moving in the buffer strips if the clearcuts are barriers to movement. Finally, I predicted that (4) the number of captures would be highest near the clearcut edges of buffer strips, because birds might perceive the clearcut area as a barrier and then progress along the edge.

I used the term 'movement' in a broad sense in my predictions. However, songbirds move for different reasons at various stages of their lives, and each of these types of movement probably does not have the same effect on the dynamics of a local population. Accordingly, I defined five types of movement: (1) within a territory, (2) off-territory explorations (Nolan 1978), (3) breeding dispersal (including pre- and post-breeding), (4) natal dispersal, and (5) migratory transience (spring and fall). If birds have a behavioral reluctance to cross open areas, the frequency of some or all of these types of movements may be altered by my treatment.

3.1 Methods

3.1.1 Experimental Design

This study was conducted near Calling Lake, Alberta (55°15′ N, 113°35′ W), in the boreal mixedwood forest region (Rowe 1972). The study area is dominated by mature trembling aspen and balsam poplar (*Populus tremuloides, P. balsamifera*), with low, but varying densities of white spruce (*Picea glauca*). The forests are pyrogenic (Eberhart & Woodard 1987) and range in age from 90 to 140+ years. Understorey vegetation is dominated by prickly rose (*Rosa* spp.), lowbush cranberry (*Viburnum edule*) and wild sarsaparilla (*Aralia nudicaulis*) in younger stands, and rose and alder (*Alnus tenuifolia* and *A. crispa*) in older stands. The forest has a high degree of natural patchiness because of topographic variation and the historical dominance of fire in the system.

This investigation is part of a large-scale experimental fragmentation study in the same area (Schmiegelow & Hannon 1993). The riparian strips are 100-m wide buffers left uncut along lakes, typically consisting of 1-5 m of riparian vegetation and 90-110 m of upland forest. The buffers form connections between forest fragments and the surrounding continuous forest (Fig. 3-1, intermediate scale). The clearcuts in my study area generally have very few standing individual trees and clumps. They isolate forest reserves from surrounding areas by a minimum of 200 m (Fig. 3-1).

I used mist net lanes as wide as each buffer strip to capture birds moving through the understorey. Each net lane had eight 12 m × 2 m nets (30 mm mesh), strung

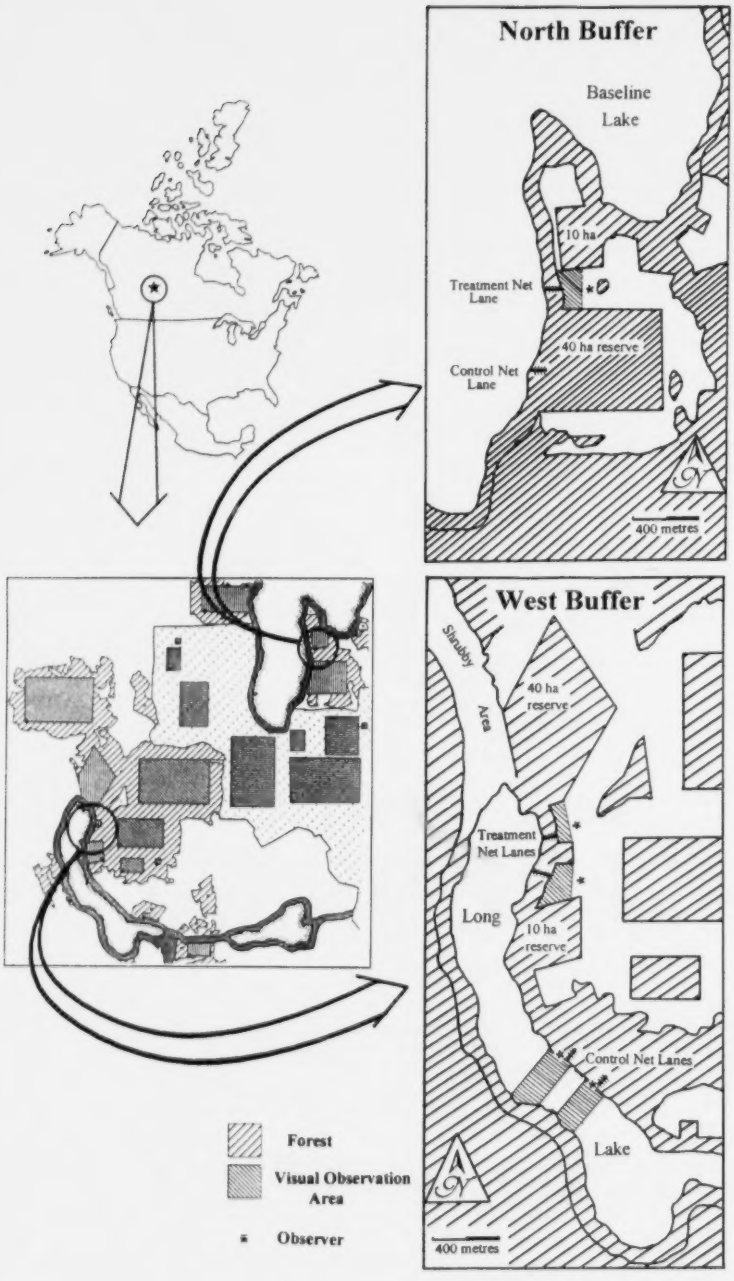

Figure 3-1. Position of and layout of mist netting sites within an experimental township (see Schmiegelow & Hannon 1993) and within north-central Alberta, Canada.

consecutively from the riparian edge to the clearcut edge (net stretch was sufficient to account for minor width variation of sites). The experiment was conducted for three years (1993-1995). I monitored one site before and after harvest (1993-1995), and three additional sites after harvest (1994-1995). The first site, hereafter called the "west buffer treatment", is a 600-m long buffer strip that connects a 10 ha and a 40 ha reserve (Fig. 3-1). Two mist net lanes were erected perpendicular to the long axis of the buffer. The two were placed 200 m from each reserve, and were therefore separated by 200 m. Site 2, hereafter called the "west buffer control", was monitored during 1994 and 1995 to act as a spatial control for the west buffer. It was located along the same lake as the west buffer treatment (Fig. 3-1), was on the edge of a forest patch that was approximately 100 ha in area, and had no harvesting near the lake. There, two net lanes were erected as in the west buffer treatment, also separated by 200 m. The two other sites added after 1993 were at a different lake, northeast of the west buffer sites (Fig. 3-1). There, the buffer strip connecting a 40 ha and a 10 ha reserve was only 200 m long (Fig. 3-1), therefore each of sites 3 and 4 ("north buffer treatment" and "north buffer control" respectively) had only one net lane. Since all of my net lanes were only capturing birds moving in the lower strata, I recognize that the capture rate was only an index and not an absolute measure of bird movements.

Each net lane was monitored from the last week of May to the first week of August. After 1993, I added one netting session before adults had settled onto territories (May 20). The nets were opened once every ten days before July and then once every five days until I finished in August. I increased netting effort after the beginning of July to increase the likelihood of intercepting dispersing juveniles. I decided *a priori* to consider adult and juvenile captures separately since they may be moving for different reasons. Netting stopped when migration started; peak migration is mid-August at a banding station 200 km south of my study site (Jungkind 1990) and at the beginning of August at a banding station approximately 100 km west of my study site (P. Rowell, pers. comm.). Nets were opened within 30 minutes after sunrise and were checked every 15-20 minutes for six hours per session. The following information was recorded for each capture:

location (net lane and position from lakeshore), time, species, age, and sex. Age and sex were determined following Pyle et al. (1987). Each bird was banded with both a numbered metal band and a colour band; the colour was different for each of the six net lanes.

I assumed that the number of birds captured would be a function of their local density. To account for this, I spot mapped (Bibby et al. 1992) the territories of all birds present in buffer strips and controls where I netted (7 ha at both west buffer sites and 6 ha at both north buffer sites). I also mapped territories in the reserves adjoining the buffer strips, since they would be the nearest potential source of birds moving through the buffers. Each buffer strip and 10-ha reserve was mapped completely, while each 40 ha plot had a 10 ha plot nested within its centre. Each area was visited eight times during late-May and June. The minimum requirement for a territory was two registrations separated by at least ten days (Bibby et al. 1992).

To determine movement rates through clearcuts, I conducted visual observations of birds in the clearcuts adjacent to the buffer strips. I did not believe erecting mist nets in the clearcuts would have allowed a valid comparison, as birds were more likely to see the nets, due to the stronger winds and lack of cover. While waiting between net checks, observers sat in the clearcuts adjacent to the buffer strips approximately 120 m from the forest edge. Topography at the north buffer treatment constrained us to observing at 80 m from the forest edge. All birds seen or heard during this time were recorded, noting species, behavior and approximate height (a 2-m pole was placed in the clearcut to compare to imaginary nets). Though I mainly faced the forest, I also recorded any birds I noted beyond 100 m from the forest edge. At the north buffer treatment, a small clump of trees was left (*ca.* 0.2-ha) between the two reserves (Fig. 3-1). Though it was behind the observer, I consistently noted any activity there. At each clearcut, an area 200 m wide was observed. At the north buffer, this was the distance between the two reserves, and at the west buffer, it was the distance between the 1 ha reserve halfway along the buffer strip and either larger reserve (Fig. 3-1). To add to my understanding of how birds react to open spaces, I also recorded the species and number of individuals of all birds moving across two 100 m wide strips of Long Lake (300 m across) by the west buffer control (Fig. 3-1).

3.1.2 Statistical Analyses

For all analyses of captures of adults and juveniles, I used only first-time captures and excluded the first session of netting in 1994 and 1995. The first session was an attempt to collect data on prebreeding movement and many birds captured during this session were transients. Capture data from the two net lanes at each west buffer site were pooled (additively) to provide single capture metrics for each location. Data from the west and north buffer sites were not pooled. I considered these sites as two different case studies rather than replicates, since the configuration of forests was substantially different between the two sites (Fig. 3-1).

To compare the number of captures of each species at the same site between years, I used a Wilcoxon Matched-Pairs Signed-Ranks test (Z statistic value). Test statistics between sites for capture rates were calculated with a Mann-Whitney U test, using the number of captures per day, correcting for local bird density by dividing captures by the number of territories of species captured in each buffer strip. To avoid Type II errors associated with low sample sizes, I accepted $p \leq 0.10$ as a significant effect.

In the analyses, clearcut observations included all birds seen at any height, but only within 100 m of the forest edge. To compare clearcut observations to movements in buffer strips, I used only data from the 10 species captured most frequently in the buffer strips, based on the sum of all captures or recaptures of adults or juveniles in the treatment buffers in 1994 and 1995, including all netting sessions. The associated probability was calculated with a Mann-Whitney U test. I used a Wilcoxon Matched-Pairs Signed-Ranks test to detect between year differences in hourly observation rates in the clearcuts. Since the north buffer observation site was only 80 m wide, a 1.25× correction factor was applied to observations before statistical comparisons with the observation sites at the west buffer treatment were made.

Recapture totals scored individuals once, though they may have been recaptured several times. Recapture data only included adults, as only 7 of 126 juveniles were ever captured again in all three years at all treatment and control locations in the study area. Test statistics on the proportional differences were calculated using a G-Test.

The data on the spatial distribution of captures within buffer strips included all captures and recaptures of adults and juveniles from all netting sessions, but excluded a subset of six species I considered riparian specialists (Northern Waterthrush, Common Yellowthroat, Wilson's Warbler, Swamp Sparrow, Song Sparrow and Red-winged Blackbird; scientific names in Appendix 2). I classified these species as riparian specialists based on their absence from point count surveys conducted in forest >100 m away from waterbodies (Schmiegelow, Machtans and Hannon unpublished data), habitat preferences listed in Ehrlich et al. (1988), and personal experience.

The regression of captures on territories was calculated on the total number of first-time adult captures after the pre-settlement net session and the total number of territories of those species in all buffer strips, split by treatment and control net lanes. Both the number of territories and captures of each species were $\log(x + 1)$ transformed prior to analysis. I used an analysis of variance to test for slope equality by including a capture × territory interaction term and tested intercept differences with an analysis of covariance.

3.2 Results

3.2.1 Pre-harvest/Post-harvest Comparison, West Buffer Treatment

At the west buffer treatment in 1993, I captured 8 juveniles and 62 adults (Table 3-1, species in Appendix 2). Adult captures decreased significantly immediately following harvesting, but increased strongly in the second post-harvest year (Table 3-1). Adult capture rates were highest in late June (Fig. 3-2*a*).

I captured significantly more juveniles (Table 3-1) in both post-harvest years. The number captured in both post-harvest years was similar. None of these species was a riparian specialist as defined in the *Methods* section. Juvenile capture rates were highest in mid to late-July (Fig. 3-2*b*). Twelve of 47 (25.5%) juveniles captured at the west buffer treatment were different species than those with territories in the buffer strip.

The number of territories in the buffer strip was significantly lower in the pre-harvest year than in the two following years (Table 3-1). The number of territories of the same species in the adjoining two reserves (Fig. 3-1) varied between years, but was highest in 1994 (1993-95: 39, 46.5, 35; 93 = 94&95, $Z < -1.467$, $p > 0.142$; 94 > 95,

Table 3-1. *Summary of total captures, number of territories of the species captured in the buffer strips and daily mean captures/territory for all sites and years Test statistics for each* p-*value are listed at the bottom of the table.*

			Number of Captures[a] (No. Territories[b])				*Mean Captures/Territory Per Day (n = 11)*		
Location	*Age*	*Year*	*Treatment*	*Between Year Differences[c]*	*Control*	*Between Year Differences[c]*	*Treatment*	*Control*	*Difference[d]*
West Buffer									
		1993	62 (27.5)	93/94 p_1=0.023 (p_7=0.067)	*no data*		0.20	*no data*	
	Adults	1994	39 (38.5)	94/95 p_2=0.001 (p_8=0.807)	34 (14.5)	p_{10}=0.167 (p_{12}=0.624)	0.09	0.21	p_{13}=0.221
		1995	100(41.5)	93/95 p_3=0.011 (p_9=0.079)	48 (17.0)		0.22	0.26	p_{14}=0.645
		1993	8	93/94 p_4=0.069	*no data*				
	Juveniles	1994	21	94/95 p_5=0.799	13	p_{11}=0.441			n/a[e]
		1995	18	93/95 p_6=0.059	12				
North Buffer									
	Adults	1994	49 (41.0)	p_{15}=0.007 (p_{17}=0.8613)	32 (31.0)	p_{18}=0.008 (p_{20}=0.683)	0.11	0.09	p_{21}=0.817
		1995	83 (39.5)		69 (28.5)		0.22	0.22	p_{22}=0.622
	Juveniles	1994	12	p_{16}=0.799	10	p_{19}=0.363			n/a[e]
		1995	16		16				

[a] *Excludes captures in first netting period (pre-settlement).*

[b] *Total number of territories of any species captured at each location throughout study.*

[c] *Wilcoxon Matched-Pairs Signed-Ranks Test on number of each species caught in each year. West buffer treatment adults n=31 species, juveniles n=14 species. West buffer control adults n=24 spp., juveniles n=11 spp. North buffer treatment adults n=25 spp., juveniles n=11 spp. North buffer control adults n=26 spp., juveniles n=15 spp.*

[d] *Mann Whitney U Test*

[e] *Sample sizes too low for reliable between-site test on either species level or daily captures.*

Test Statistics: $Z_1 = -2.275$, $Z_2 = -3.328$, $Z_3 = -2.2557$, $Z_4 = -1.820$, $Z_5 = -0.255$, $Z_6 = -1.886$, $Z_7 = -1.835$, $Z_8 = -0.245$, $Z_9 = -1.758$, $Z_{10} = -1.384$, $Z_{11} = -0.770$, $Z_{12} = -0.490$, $U_{13} = 42.0$, $U_{14} = 53.5$, $Z_{15} = -2.714$, $Z_{16} = -0.255$, $Z_{17} = -0.175$, $Z_{18} = -2.646$, $Z_{19} = -0.910$, $Z_{20} = -0.408$, $U_{21} = 57.0$, $U_{22} = 53.0$.

$Z_{94/95} = -1.726, p = 0.084$).

The recapture rate (number recaptured/total captures) was 12.9% (8/62) in the pre-harvest year. There were significantly more ($G > 8.77, p < 0.003$) recaptures in both years after adjacent harvest (1994: 18/39 = 46.2%, 1995: 33/100 = 33.0%). Recapture rates did not differ significantly between the two post-harvest years ($G = 2.06, p = 0.155$).

3.2.2 Treatment Versus Control Buffer: West Buffer Sites

In both 1994 and 1995, more birds were captured in the treatment than in the control for adults and juveniles (Table 3-1). However, once local density was corrected for (see analysis below) by dividing captures by territories, the daily capture ratios of adults were similar (Table 3-1). The daily mean was lower in the treatment in 1994, but not significantly so. The pre-harvest capture ratio in the treatment was similar to both the 1994 and 1995 data from the control ($U \geq 45.5, p \geq 0.324$). Since the species composition of juveniles was different between sites (7 of 18 species in common) and juveniles were captured on only eight of the 12 netting days, a reliable statistical comparison cannot be made. However, the number of territories was a poor predictor of the number of juveniles captured (see *Relationship Between Territories and Captures* below).

The number of captures per species of adults and juveniles did not differ between years in the control buffer. The increase in adult captures observed in the treatment buffer between 1994 and 1995 also occurred in the control buffer, but the increase was not significant (Table 3-1). The number of juveniles captured changed very little (Table 3-1).

The timing of captures differed for juveniles between the treatment and control. In 1994, most juveniles were caught later at the control (early August, Fig 2*b* & *d*) than at the treatment, where most juveniles were captured in mid to late-July (Fig. 3-2*b*). In 1995, the difference was not significant, due to the capture of a family group of Dark-eyed Juncos early in the season in the control.

The number of territories in the control buffer increased a nonsignificant amount from 1994 to 1995 (Table 3-1). As in the west buffer treatment, the increase in territories

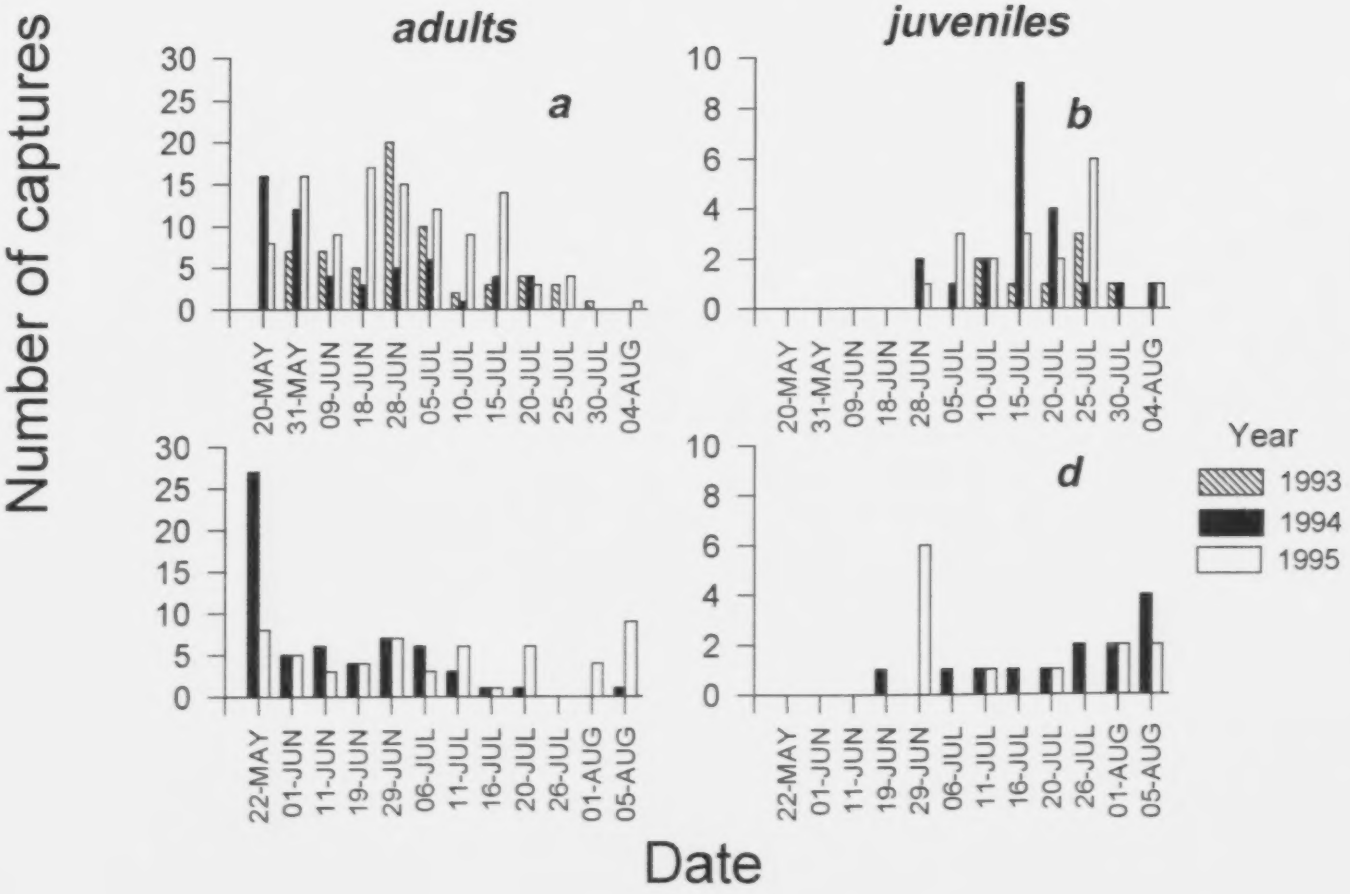

Figure 3-2. Temporal distribution of captures of adults and juveniles in the west buffer treatment site.(a & b), west buffer control site (c & d). The temporal distribution of juveniles was different in 1994 ($U = 83.0$, $p = 0.054$), but statistically similar in 1995 ($U = 90.0$, $p = 0.441$).

between 1994 and 1995 was proportionately smaller than the increase in captures. The percentage of recaptures in the control were nonsignificantly lower than the treatment in both 1994 and 1995. In 1994, the treatment recapture ratio was 46.2% and the control was 29.4% (10/34) ($G = 2.18$, $p = 0.144$). In 1995, the treatment dropped to 33.0% and the control to 25.0% (12/48) ($G = 1.00$, $p = 0.321$). Like the decrease at the treatment site described earlier, the between-year decrease at the control site was nonsignificant ($G = 0.196$, $p = 0.662$).

3.2.3 Treatment Versus Control Buffer: North Buffer Sites

In both 1994 and 1995, more adults were captured in the treatment than the control (Table 3-1, Fig. 3-3*a* & *c*). However, like the west buffer sites, the daily capture ratios for adults were similar for both years (Table 3-1) once local density was corrected for. There were significantly more adults captured in 1995 at both the treatment and control sites (Table 3-1).

The number of juveniles captured did not differ significantly in either year within the treatment or control (Table 3-1; Fig. 3-3*b* & *d*). Also, the timing of captures did not differ between treatment or control within or between years (Fig. 3-3*b* & *d*). Like the west buffer sites, the species composition of juveniles was not similar between north buffer sites (4 of 22 species in common) and they were captured on (at most) seven of 12 netting days (Fig. 3-3*b* & *d*). Therefore a reliable statistical comparison between captures per day or species was not possible.

The number of territories of captured species in both the treatment and control buffer were similar between 1994 and 1995 (Table 3-1). The number of territories in the surrounding reserves (Fig. 3-1) also did not change significantly (76.5 to 83.0; $Z = -0.4708$, $p = 0.638$). The slight decrease in the number of territories and the significant increase in the number of captures at the north buffer sites made the inequality between the number of captures and territories observed in 1995 greatest at the north buffer sites.

The percentage of recaptures did not differ significantly between treatment or control within or between years (treat×year, 8/49 to 13/83, $G = 0.010$, $p = 0.921$; control×year, 8/32 to 14/69, $G = 0.280$, $p = 0.602$; treat×control (1994), $G = 0.904$,

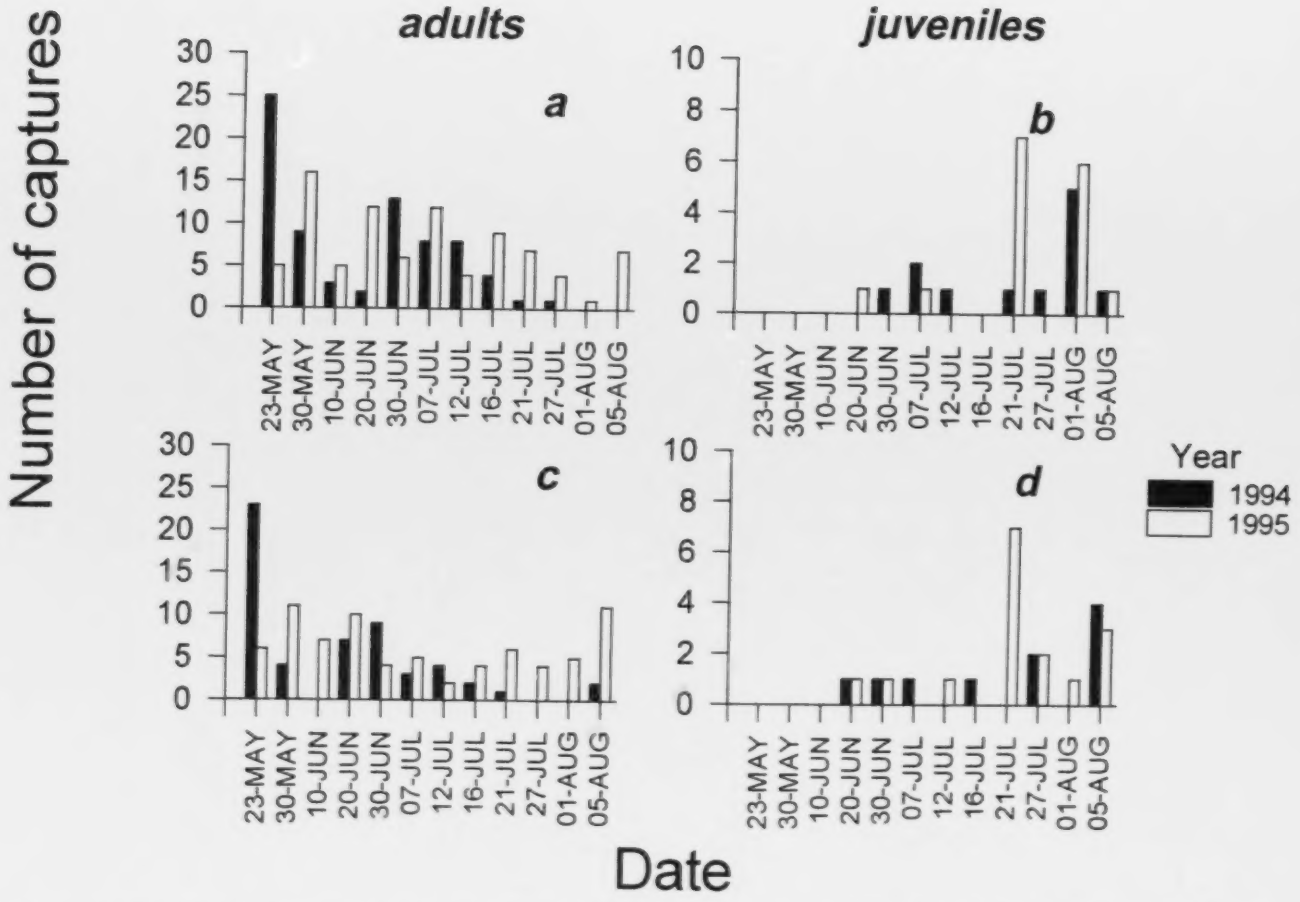

Figure 3-3. Temporal distribution of captures of adults and juveniles in the north buffer treatment site (a & b), and the north buffer control site (c &d). There were no differences in the temporal distribution of juvenile captures within or between sites (treat × year, $U = 96.0$, $p = 1.00$; control × year, $U = 72.5$, $p = 0.686$; treat × control (1994), $U = 55.0$, $p = 0.738$; treat × control (1995), $U = 118.5$, $p = 0.707$).

$p = 0.350$; treat×control (1995), $G = 0.550$, $p = 0.463$). The trend for an overall decrease in recaptures evident at the west buffer sites was also observed at both north buffer sites.

3.2.4 Movement Comparison Between Buffer Strips, Clearcuts and Lakes

The ten species most commonly captured in mist nets were observed significantly less frequently in clearcuts (Table 3-2). The comparison is conservative in favour of the clearcuts; I compiled all bird observations within 100 m (the width of a net lane), but also included birds seen at any height (80.5% of birds were observed at >2 m). If only the observations of birds seen at heights ≤2 m were used, the disparity between movements in clearcuts and buffer strips was greater ($U = 14.0$, $p = 0.006$). Additionally, clearcut observations recorded any individual seen within the 100×200 m area adjacent to each of the three treatment net lanes. The number of birds that would have actually been intercepted by a net lane placed in a clearcut would have been lower still.

Thirty-five species were observed in clearcuts (Appendix 2). However, five species (Cedar Waxwing, Pine Siskin, White-throated Sparrow, Red-winged Blackbird, Yellow-bellied Sapsucker) accounted for 65.4% of observations. The White-throated Sparrow nested in the clearcuts but used the buffer strips (pairs nesting in clearcuts were captured in the net lanes), and Yellow-bellied Sapsuckers foraged on remnant birch (*Betula* spp.) trees in left uncut in the clearcuts, but nested in the forest. The other three species were present as transients in the clearcuts.

More birds were observed in the clearcut at the north buffer treatment than at the west buffer treatment. For observations made within 100 m, the mean number of individuals observed per hour observed in 1994 at the west buffer was 2.93 versus 5.55 at the north buffer ($U = 38.0$, $p = 0.049$). There were more birds observed at both sites in 1995, however only the west buffer showed a significant increase (west buffer to 4.19/hour (+43.0%), $Z = -1.804$, $p = 0.071$; north buffer to 7.90/hour (+42.3%), $Z = -0.078$, $p = 0.938$). The mean number of observations made at the west and north buffer clearcuts did not differ significantly in 1995 ($U = 58.0$, $p = 0.419$). The higher ratio at the north buffer treatment in 1995 was due primarily to two observation periods with large numbers of birds seen, while the distribution was more uniform at the west buffer.

Table 3-2. Comparison of capture rates of the 10 most frequently captured species in treatments (1994 and 1995) with their observation rate in adjacent clearcuts.

	Mist Net Lanes (N = 3)		*Clearcuts (N = 3)*	
Species	*Number Captured*[a]	*Captures per hour*[b]	*Number Observed*[c]	*Observations per hour*[b]
Least Flycatcher	98	0.25	3	0.02
White-throated Sparrow	93	0.23	52	0.38
Ovenbird	40	0.10	0	0.00
Mourning Warbler	32	0.08	5	0.04
Swainson's Thrush	31	0.08	1	0.01
Yellow-bellied Sapsucker	24	0.06	34	0.25
Song Sparrow	20	0.05	10	0.00
Swamp Sparrow	18	0.05	0	0.00
Yellow-rumped Warbler	18	0.05	2	0.01
Yellow Warbler	18	0.05	0	0.00

[a]The mist netting totals included recaptures to compensate for the likelihood that individuals could have been recounted in the clearcuts. Both adults and juveniles are included in the totals. There was 396.0 hours of mist net effort and 137.3 hours of observation time in clearcuts.
[b]Mann-Whitney U test comparing capture rate and observation rate: U = 20.0, p = 0.023.
[c]The observations in the clearcuts counted birds at any height and within 100 m from the forest edge, over a 200 m length. See Appendix 2 for scientific names.

The number of birds moving across Long Lake (Fig. 3-1) was lower than the number observed in the clearcuts. In 122.1 hours of observation time in 1994 and 1995, 304 birds were observed flying across the lake (2.5 birds/hour)(Appendix 2). However, observations in clearcuts were not exclusive to direct transits across the site (as the lake ones had to be), so the comparison is indirect. Most of the observations (58.7%) were of Red-winged Blackbirds, Cedar Waxwings, Tree Swallows and White-winged Crossbills.

3.2.5 Spatial Distribution of Captures in Buffer Strips

The number of birds captured in a net was dependent on its distance from the lake. Birds that I classified as riparian specialists in the methods section were not included in this analysis. At all netting sites in all years, the number of captures per net increased logarithmically with its increasing proximity to the lakes (Figs. 4*a* & *b*) (pooled data, $F = 18.94$, $p = 0.003$, $R^2 = 0.73$). If the increase in capture rates near the lakeshore reflected the lateral movements of birds after they encountered a major barrier (the lake), I might

expect a similar result at the edge of clearcuts. At the west buffer treatment, following harvesting, there was no increase in birds caught in net lanes closest to clearcuts (Fig. 3-4*a*). However, in the second post-harvest year, the proportion of captures near the clearcut were more than doubled from the previous two years. When averaged across 1994 and 1995 and all sites, capture proportions near clearcuts were not higher near clearcuts for treatments than controls (Fig. 3-4*b*). There were no data to indicate that movements in any buffer were biased in one direction; neither adults nor juveniles were captured more frequently on particular sides of any net lane.

3.2.6 Relationship Between Territories and Captures

For all netting sites combined in all years, the number of adults was positively related to the number of territories present in a buffer strip (Fig. 3-5; pooled data: $F = 101.79$, $p < 0.001$, $R^2 = 0.59$, slope $= 0.72$). Over all years, the relationship did not differ if net lanes were adjacent to forests or clearcuts (Fig. 3-5; slope: $F < 0.01$, $p = 0.979$; intercept: $F = 0.23$, $p = 0.635$). However, using only the data from the first year of post-harvest observation, there were significantly fewer captures per territory in net lanes adjacent to the clearcuts (treatment sites) (intercept: $F = 11.03$, $p = 0.002$), while the general, increasing trend was similar (slope: $F = 0.04$, $p = 0.842$).

The number of territories present in a buffer strip was a poor predictor of the number of juveniles captured. For all sites and years combined, there was a significant, positive relationship ($F = 18.16$, $p = 0.0001$) between territories and captures, but the slope of 0.34 was less than half the value observed for adults and the explanatory power of the regression was low ($R^2 = 0.19$). There were no differences in the number of captures between net lanes adjacent to clearcuts (treatments) or forests (controls) (slope: $F = 0.04$, $p = 0.850$; intercept: $F = 0.30$, $p = 0.586$).

3.3 Discussion

3.3.1 Frequency of Movements in Buffer Strips Versus Temporal Controls

My first prediction was supported for juveniles but not for adults. Compared to pre-harvest numbers, more than twice as many juveniles were captured in both post-

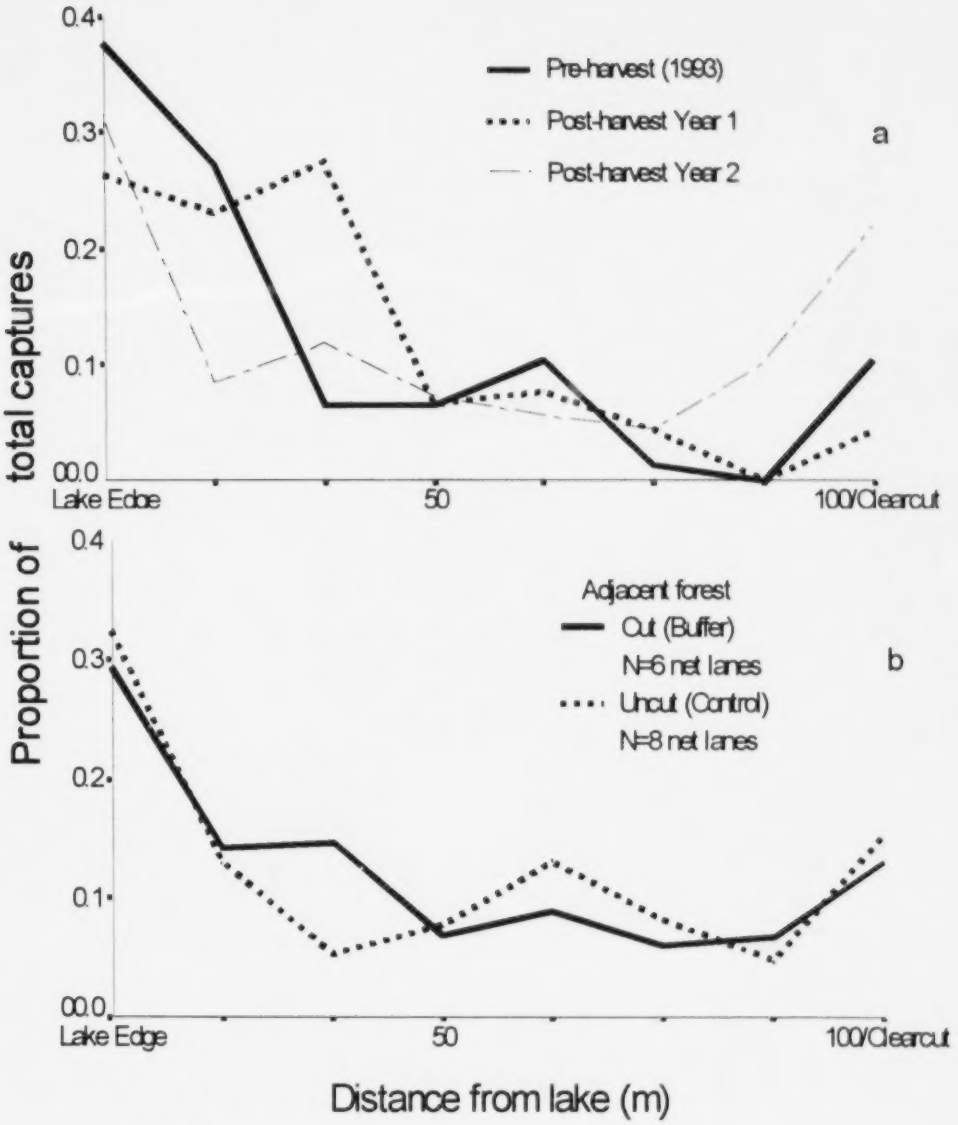

Figure 3-4. Comparison of capture distributions along nets (a) at the west buffer , pre- and post-treatment, and (b) between all net lanes adjacent to clearcuts (treatments) and net lanes adjacent to undisturbed forest (controls), for all years. The cut locations are the west buffer treatment (2 lanes) and north buffer treatment in 1994 and 1995, and the uncut locations are the west buffer control (2 lanes) and north buffer control in 1994 and 1995 and the west buffer treatment in 1993 (2 lanes, the precut year).

harvest years in the west buffer treatment. Since the number of juveniles captured was poorly predicted by the number of adult territories, they likely represent natal dispersers. The timing of captures (mid to late July) and the fact that so few juveniles were recaptured during the same year supports this conclusion. This interpretation is also substantiated by the species composition of juvenile captures; in 1994, seven ovenbirds were captured in the west buffer treatment, yet there was only one ovenbird territory, where a maximum of five or six young could have fledged. Lastly, even though I could not determine if juveniles captured were born in territories in the buffer strip or nearby, at least 25.5% of the juveniles captured represented species that did not hold territories in the buffer strip.

3.3.2 Frequency of Movements in Buffer Strips Versus Spatial Controls

My second prediction was only supported for juveniles at the west buffer treatment and not for adults or juveniles at other sites. At the west buffer treatment, there were >50% more captures than at the west buffer control, both in 1994 and 1995. Additionally, the timing of capture peaks was different at the two sites, suggesting two different types of movements. At the west buffer treatment, most juveniles were captured around mid-July, roughly coincident with the time when birds born in late June would be leaving their natal territories. This allows a one to two week fledgling period (Ehrlich et al. 1988) and an additional week of movements within the territory. At the west buffer control, most of the juveniles were captured at the end of July and the beginning of August. Birds moving this late in the season are probably in the migratory transience category of movement. I could not distinguish between the end of dispersal of locally produced juveniles and migration. However, at a banding station operating approximately 100 km to the west, the first week of August was extremely busy (12.7 birds/net hour, P. Rowell pers. comm.), indicating that migration was well underway. The possibility that a change in movement patterns (dispersal to migration) was occurring is supported by an increase in observations in clearcuts (mostly group movements) and the relatively few adult captures in July until the last or second to last netting sessions.

The similarity in the frequency and distribution of juvenile captures at the north buffer sites indicates that the buffer strip was supporting the same number of movements

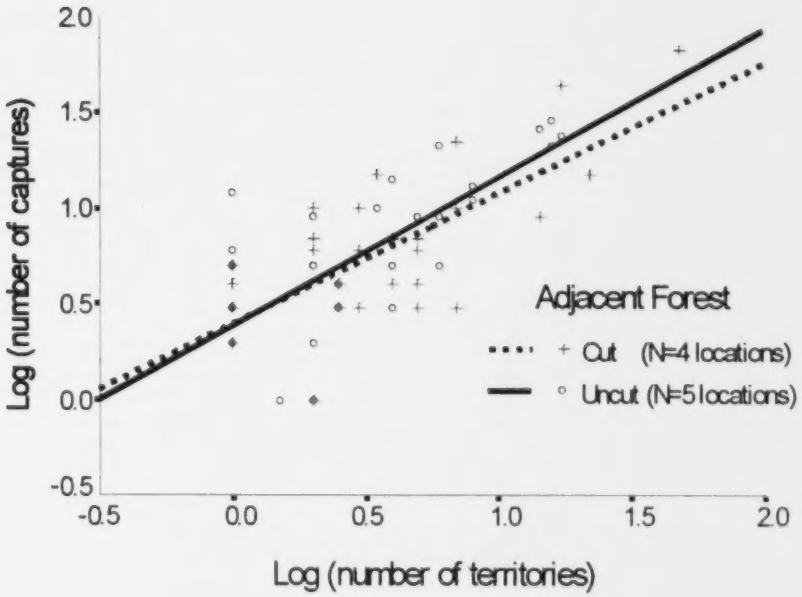

Figure 3-5. Relationship between number of adults captured per territory in buffer strips, tallied by species. All sites and years were pooled for this analysis. Net lanes are grouped as cut and uncut as for Fig. 3-4.

as the undisturbed control site. However, the control site could potentially intercept individuals as they move from the larger reserve to the lakeside forest, where the net lane is located, as well as those moving along the buffer strip. The north buffer treatment still acts as a corridor, but does not concentrate movements as the west buffer treatment appeared to do.

Two alternative explanations could account for my results. The first is that the variation in the west buffer treatment is spurious and not related to the treatment since the north buffer showed no effect. A second alternative explanation for the increased number of juveniles captured in the west buffer after treatment is an increase in reproductive success after harvest, from pre-harvest levels (1993). I reject the first alternative based on the higher number of birds observed moving through the clearcut at the north buffer treatment, which indicates that corridor use may be less significant there. Bird activity was frequently noted in the small patch of forest in the clearcut between the reserves (Fig. 3-1), indicating that it might have been a stepping stone for movements. I reject the second alternative because data on reproductive success in American Redstarts (*Setophaga ruticilla*) collected in 1993, 1994, and 1995 in my study area do not support this explanation. Nest abandonment increased and fewer young were fledged per successful nest in both post-harvest years (M.-A. Villard and S.J. Hannon, unpublished data). I do not, however, have indicators of productivity for other species in the study area.

My first and second predictions were not supported for adults. At my temporal control, the number of captures decreased in the first post-harvest year and the proportion of recaptures increased in both post-harvest years. A higher recapture rate suggests that there were proportionately fewer transient birds. Practically no birds were so mobile that they were captured at a different buffer strip (between any treatment and control) than the one where they were originally captured (6/760). The higher capture rates at pre-harvest west buffer treatment (1993) and west buffer control (1994) may reflect the fact that the forest adjacent to the lanes contained a pool of birds which might have been captured when they were on off-territory explorations (Nolan 1978). Following harvesting, the pool of exploring birds would have been smaller or absent, as supported by my analysis of

territory density in buffer strips and capture rates for the first post-harvest year. In 1995, the increase in captures was a year effect observed at all sites. Rapid clearcut regeneration (a source of cover and food near the forest edge) might have also contributed to the increased capture rates at treatment net lanes.

The relationship between territories and captures suggests that most of the adults captured were likely residents of the buffer strips, making the conservation value of the buffers greater than if the corridors were only used for movement. Adult capture frequencies were highest (after the pre-settlement session) during late June at all sites, the time when adults would be foraging to feed nestlings. The patterns suggest that the value of the treatment buffers as foraging areas was not negatively affected by adjacent cutting.

3.3.3 Frequency of Movements in Clearcuts Versus Buffer Strips

My third prediction was supported. Of the ten most frequently captured forest species, I only saw White-throated Sparrows and Yellow-bellied Sapsuckers using the clearcut for nesting and foraging respectively. The species that were commonly seen in the clearcuts are ones that either are typically associated with forest-edge or open habitats or that are itinerant during the breeding season. This result is in agreement with Haas (1995). In her study, movements of birds occurred significantly more often between connected shelterbelts, or within a shelterbelt, compared to movements between shelterbelts that were separated by agricultural lands.

For adult captures at all locations and for juvenile captures at the north buffer sites, capture rates were similar in treatments and controls. Though no increase was observed, the corridors still maintain at least as much movement activity as control sites. Based on my movement comparisons with clearcuts, the link between reserves is broken by clearcuts for forest birds, emphasizing the use of corridors.

3.3.4 Frequency of Movements Relative to Clearcut Edge

My last prediction was only partially supported. It was correct for nets close to lakes, but not for nets close to clearcuts. The only difference was recorded at the west buffer treatment in 1995. Clearcut regeneration in the deciduous cutblocks is rapid (>1.5 m in 1995); the abruptness of the edge and the value of the clearcut edge as a resource for

cover and food may be the cause of the increase. I also observed >40% more birds in the clearcuts from 1994 to 1995, further supporting a decreased level of avoidance.

I propose a two-part explanation for the higher number of captures near the lake. First, birds were seen moving across lakes much less often than across 200-m wide clearcuts where they could perch on scattered trees left standing. Excluding the four species most frequently seen crossing lakes, very few birds were observed crossing the 300-m wide lake (1.2 birds per hour). The lake is a functionally impermeable barrier for most species of forest birds. Though in a different system, Willis (1974:166) noted that tropical antbirds were "unable to...cross water gaps, even of a few hundred metres." Second, the greater capture rates I obtained near the lakes may reflect the higher insect abundance ofter found at the edge of water bodies. Jackson and Fisher (1986) found that a stream produced several orders of magnitude more insects than terrestrial sites, and would be an area of abundant prey for insectivorous birds. Also, Gray (1993) found that riparian insectivore (bird) densities were correlated with insect production in the aquatic system, and noted in his study that birds frequently foraged near the stream. The combination of the two factors, with the increased availability of resources as the main reason, explains my results.

3.4 Conclusions and Research Recommendations

Overall, my findings demonstrate that corridors are used more frequently than clearcuts by forest bird species for movement and that, at the very least, they can maintain the movement rates observed in undisturbed sites. Secondly, movements of some species truly represented natal dispersal through corridors. Because the result was not replicated, I cannot conclusively say that juvenile movements will increase in all buffer strips after disturbance of adjacent habitat. However that was definitely the case in my pre- and post-disturbance site. Also, the direct comparison between movements observed in clearcuts and frequency of capture is only qualitative, but very conservative in favour of the clearcuts.

I admit that my design was less than perfect in several ways. First, I was only able to establish one before and after treatment site. Second, the configuration of forests near

my two lakes was different. The north buffer led away from a peninsula (Fig.3-1), which might have had a smaller source population than the west buffer. The relatively short north buffer could only accommodate one net lane. With a longer buffer and two net lanes at the site, some different trends may have been evident. For example, at the west buffer treatment, the net lanes reversed their proportions of total captures between 1993 and 1994. More replication would presumably alleviate these problems, but would make the experiment unmanageably large and expensive.

I believe the pre- and post-treatment approach used in my experiment should be an important component of future research on corridor use, as it reveals patterns not easily discernable by only recording post-disturbance results with control areas deemed to be similar. One suggestion for future research would include taking advantage of new micro-electronic transmitters to track juvenile movements out of areas with corridors and areas without corridors. However, the long-term monitoring of the forest fragments that are connected by my buffer strips is another critical component of the experiment. The results will reveal if movements in the buffers actually affect population demography in the fragments. This will provide the indirect test of the corridor hypothesis; if my results are valid, the fragments connected by corridors will either retain more forest species or may keep them in greater abundance than fragments without corridor connections.

Inglis and Underwood (1992) made several comments concerning the design of experiments to test the use of corridors. The difficulty of making homogeneous replicates, having very labour intensive investigations and low sample sizes were all difficulties evident in my study. The myriad of species which may or may not use corridors and the specific circumstances governing when they will use them makes answering the 'corridor question' very difficult. Undisputable evidence of corridor value is probably species dependent and will require many more experiments.

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Chapter 4

Thesis Discussion

4.0 Summary of Results

The purpose of my research was to assess the value of buffer strips[3] as songbird habitat, assess how songbird communities were affected (short-term response) by harvesting adjacent to buffer strips and to determine if songbirds used buffer strips as movement corridors.

I found that forests adjacent to watercourses supported more species and individuals than similar upland forest. The difference was still evident when species that were riparian specialists were removed from analyses. Further, forests adjacent to watercourses supported a unique assemblage of species. They contained nearly all the species that upland forest did, but the lake-side forests contained several species that were significantly more abundant than in upland forest. Brown-headed cowbirds were significantly more abundant in forests adjacent to watercourses, whether forests were vegetatively similar or not.

The immediate effects of adjacent harvesting on the songbird communities in buffer strips were minimal. Species richness, abundance and relative turnover were not significantly affected by harvesting. One species was clearly affected by harvesting; the abundance of ovenbirds declined significantly. Before harvesting, ovenbird territories were located away from the riparian edge, often having their full perimeter only partially within 100 m of the edge (post-harvest buffer/clearcut boundary). No ovenbirds had a full territory in any of the 100-m wide buffer strips I surveyed after adjacent harvesting, and the one territory in the west buffer was where a 1 ha reserve effectively increased the buffer width to 200 m.

Significantly more juveniles moved through one of the buffer strips after the

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3

Riparian buffer strips are areas of forest left along watercourses after timber harvesting, primarily to protect water quality. Because the buffer strips in this study contained primarily upland species and structure, they were not referred to as riparian forest.

adjacent forest was removed, suggesting a funnelling effect. As many birds moved through buffer strips as through undisturbed forest. Recapture rates of adults in buffer strips were typically higher than in undisturbed forest, indicating that many of the birds captured were probably resident in the buffer strip or nearby forest. The relationship between the number of adult territories and the number of juvenile captures was weak, indicating that captured juveniles were probably dispersing individuals.

Of the bird species captured most often in the buffer strips, significantly fewer were observed moving across the clearcut separating forest fragments. This suggests that the clearcuts were a barrier to movement and unsuitable habitat for some species. The number of birds observed crossing clearcuts was higher when the distance between reserves was shorter, strengthening the argument that, at some threshold distance, birds become more reluctant to cross open spaces. Similarly, comparatively few birds were seen flying across a 300-m wide lake; most of those observed were not forest species.

4.1 Significance of Results

4.1.1 Buffer Strip Value: Habitat and Corridors

The conclusion that buffer strips have high value as habitat and are useful as corridors for adults and dispersing juveniles is evidence that they can play an important role in the conservation of songbirds in the boreal mixedwood. Forest management plans that have a goal of conserving songbirds will be able to use buffer strips as a tool that may help lessen the impact of fragmentation on species using older forest. Buffer strips will not ever be able to maintain the pre-disturbance abundance and diversity of any given area, since substantial habitat loss will still be occurring because of harvesting.

One caveat remains on describing lake-side forest as more valuable than upland forest; richness and abundance may not be good indicators of habitat value (Van Horne 1983). However, for my study, three factors indicate the two measures may suffice. First, the study was conducted over two years, helping to lessen the effect of annual variation. Second, temporal and spatial controls were used, with coincidental upland comparisons. Third, the pairing success of ovenbirds was not affected by harvesting (C.S. Machtans unpublished data, Appendix 3). I therefore use the higher number of individuals and

species using the lake-side forest to define it as higher quality, or more valuable, habitat for songbirds than similar upland forest.

Lake-side forest should be a priority for conservation using the above definition of value. If leave areas are larger than 100-m wide buffer strips, it would be better have leave areas adjacent to watercourses. Forest managers are often forced to choose alternatives from a set that all carry detrimental, or at least unknown, effects to the species in an ecosystem. Leaving forests near watercourses provides an alternative that may help lessen the overall negative effects of harvesting on songbirds using mature and old forest. However, the apparent value of the forest near watercourses must be tempered with the knowledge that nest parasitism may be highest there, and that buffer strips will become unnaturally old if all disturbance regimes are excluded. With fire suppression preventing natural regeneration, some type of rotating harvest system or prescribed burn program would be probably be necessary maintain the value of buffer strips. Further, previous research indicates that maximizing buffer width will provide habitat for more forest bird species (i.e. Stauffer and Best 1980, Darveau et al. 1995).

4.1.2 Corridor Function

The use of the buffer strips as corridors, and the low frequency of movement across clearcuts, have important implications for reserve design. The populations left on the landscape after harvesting will have several practical similarities to a theoretical regional metapopulation; songbird populations of various sizes will be isolated by varying degrees of distance and difficulty of movement between patches.

The biases in emigration and immigration rates created by distance and degree of connection is represented in Fig. 4-1 and Fig. 4-2. The hypothetical immigration and emigration rates of prospective breeders is approximately equal before fragmentation (Fig. 4-1, times A, B, C). There are more black arrows coming into the patch in 'A' since immigrants arrive from all sides of the artificially delineated forest patch, but does not necessarily indicate that more will stay. Assuming that territory selection occurs primarily before fall migration (see references in Chapter 3), then spring immigrants (D) return to the fragment selected in 'C'. At the end of that breeding season (E), locally produced

young leave the fragment to find breeding territories away from their natal territories. The number of immigrants decreases (black arrows, E) however, because young are now reluctant to cross the clearcuts to find the fragment. Consequently, the number of returning breeders diminishes (F), local production is similarly affected (white arrows, G) and the number of immigrants remains small (black arrows, G). If isolation did not affect the number of immigrants (small isolation distance or matix not completely hostile), the quality of immigrants arriving in fragments may be lower than in continuous forest (Lens and Dhondt 1994). This could also decrease the reproductive output of the birds using the fragment.

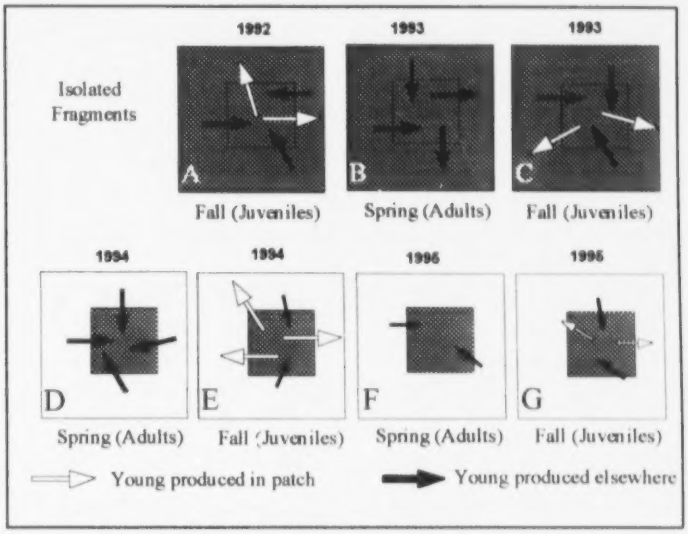

Figure 1. Diagrammatic representation of emigration and immigration for a forest patch (shaded) that becomes completely isolated by harvesting after time 'C'. The size of the arrows is an indication of the magnitude of movement rates.

Emigration and immigration rates are better maintained when the fragment is connected to other similar habitat with a corridor (Fig. 4-2). Before being isolated (times A, B,C), rates are the same as for the pre-disturbance forest in Fig. 4-1. The corridor provides a conduit that keeps immigration and emigration levels higher (than for completely isolated forest) following fragmentation (times E and G). Consequently, local settlement (and therefore the production of young in the fragment) is enhanced relative to completely isolated fragments by the maintenance of dispersal events. This might be manifested as either, or both, higher abundances and species richness in the connected reserves.

Empirical testing of the actual effects of corridor presence has begun. A three-year experiment (Schmiegelow et al. in review) documented species composition and abundance in forest fragments completely isolated by clearcuts and ones that remained connected with forest strips. The initial community response (2 years post-harvest) was less pronounced in reserves connected by corridors than completely isolated reserves. The negative effects observed in the isolated fragments, but not in the connected fragments included: higher species turnover, area-dependent diversity, and a greater than expected number of Neotropical migrants showing an abundance decline.

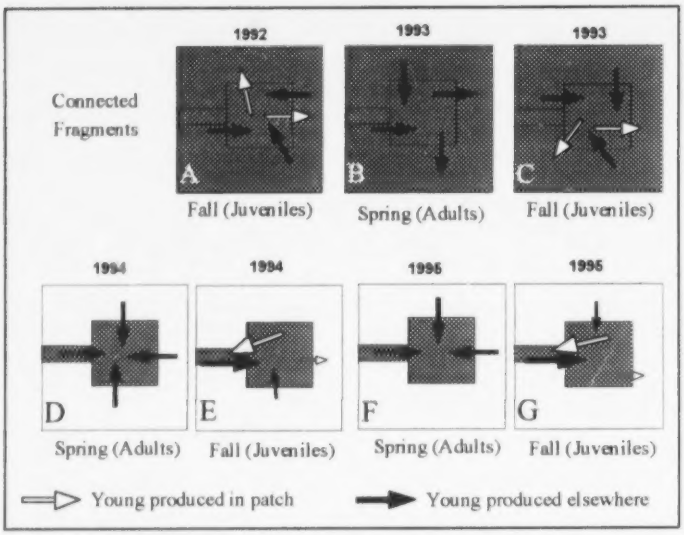

Figure 2. Diagrammatic representation of emigration and immigration for a forest patch (shaded) that remains connected to other forest with a corridor. The size of the arrows is an indication of the magnitude of movement rates.

We (Schmiegelow et al.) attributed the observed patterns to a combination of two factors. First, the connected reserves all had their effective sizes increased by the addition of 100-m wide buffer strips along one side. For the two smallest reserve classes (1 and 10 ha), the increase in effective area was 100% and 40% respectively. Second, the similarity of the connected reserves to spatial controls suggests that the corridors may be functioning as theorized above, supported by the data in Chapter 3. However, determining the relative contribution of area and connectedness would be difficult in this case. An experiment where fragment residents are removed would be necessary to separate the effects.

4.2 Management Recommendations

Three recommedations to forest managers are presented below. These are intended to be useful for helping conserve songbird populations in the boreal mixedwood forest, and might not be the best recommendations for the myriad of other forest-dwelling organisms currently extant in northern Alberta. This set of management recommendations is specific to the boreal mixedwood forests of Alberta. However, research from other locales indicates that the recommendations would likely be reasonable for most forested landscapes.

Each recommendation is presented with a summary of the data that supports it. I have indicated if the data is from my research or not. The details for each bit of supporting data can be found in other sections of this thesis.

Recommendation 1: Placement of Leave Areas of Habitat

If forest type and age are the same, usually leave forest adjacent to waterbodies if there is a choice to leave it there or upland. Some upland forest must also be left.

Supporting Data:

1) Upland and riparian species will be present (Fig. 2-2, Chapter 2 text)
2) Overall number of birds and species will be higher (Table 2-3, text page 21)
3) More cowbirds and buildup of organic fuel for fires (Chapter 2 text) in buffers necessitates having reserves both upland and near watercourses until these effects can be discounted.

Recommendation 2: Buffer Strip Width

Make buffer strips wider than 100 m whenever possible. The TROLS study at the University of Alberta[4] is specifically addressing what an appropriate width will be.

[4]Contact Dr. Susan Hannon, Department of Biological Sciences for more information.

Supporting Data:

1) Wider buffer strips have more forest-dwelling birds (references on page 8 and 9)
2) Ovenbird abundance declines in 100 m buffers compared to undisturbed forest (text page 24)
3) Ovenbirds need buffer strips >175 m wide to breed (Stauffer and Best 1980)
4) Ovenbirds and some other forest birds avoid edges and small forest fragments (references for ovenbird on page 24, general fragmentation on page 1)

Recommendation 3: Habitat Connectedness

Leave uncut forest configured so that patches are connected by buffer strips.

Supporting Data:

1) Buffer strips used as corridors by juveniles (page 50-51)
2) Buffer strips maintain (Table 3-1) adult movements or enhance adult dispersal (Haas 1995)
3) Reserves connected by corridors less affected by fragmentation (Schmiegelow, Machtans and Hannon, in press, see also references on page 33-34)

4.3 Concluding Remarks

Future research in the boreal mixedwood needs to focus on more specific measures of how valuable the managed landscape is to songbirds. Data are needed on reproductive output of species in buffer strips to quantify a correlation between density and habitat quality. It must be determined how frequently nests in buffer strips are parasitised by cowbirds. If observed densities are significantly affecting local production, buffer strips might be reproductive sinks for parasitized species. Direct measures (tracking) of juvenile movements through corridors and across harvested areas is also needed to quantify dispersal movements. The dynamic nature of a regenerating landscape should also be factored into conservation plans; the absence of a permanent, completely unforested matrix will undoubtably influence the traditional fragmentation effects (nest predation,

parasitism, inter-specific competition, area effects, etc.) observed in agricultural landscapes.

4.4 Literature Cited

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Appendix 1. List of common and scientific names of all bird species in Chapter 2.

yellow-bellied sapsucker	Sphyrapicus varius
hairy woodpecker	Picoides villosus
downy woodpecker	Picoides pubescens
northern flicker	Colaptes auratus
western wood-pewee	Conotopus sordidulus
least flycatcher	Empidonax minimus
alder flycatcher	Empidonax alnorum
boreal chickadee	Parus hudsonicus
black-capped chickadee	Parus atricapillus
brown creeper	Certhia americana
red-breasted nuthatch	Sitta canadensis
house wren	Troglodytes aedon
winter wren	Troglodytes troglodytes
golden-crowned kinglet	Regulus satrapa
ruby-crowned kinglet	Regulus calendula
American robin	Turdus migratorius
hermit thrush	Catharus guttatus
Swainson's thrush	Catharus ustulatus
cedar waxwing	Bombycilla cedrorum
red-eyed vireo	Vireo olivaceous
Philadelphia vireo	Vireo philadelphicus
warbling vireo	Vireo gilvus
solitary vireo	Vireo solitarius
Tennessee warbler	Vermivora peregrina
orange-crowned warbler	Vermivora celata
black-and-white warbler	Mniotilta varia
yellow-rumped warbler (myrtle)	Dendroica coronata
magnolia warbler	Dendroica magnolia
black-throated green warbler	Dendroica virens
yellow warbler	Dendroica petechia
mourning warbler	Oporornis philadelphia
Connecticut warbler	Oporornis agilis
Canada warbler	Wilsonia canadensis
ovenbird	Seiurus aurocapillus
common yellowthroat	Geothlypis trichas
American redstart	Setophaga ruticilla
rose-breasted grosbeak	Pheucticus ludovicianus
song sparrow	Melospiza melodia
Lincoln's sparrow	Melospiza lincolnii
swamp sparrow	Melospiza georgiana
chipping sparrow	Spizella passerina
clay-colored sparrow	Spizella pallida
dark-eyed junco	Junco hyemalis
white-throated sparrow	Zonotrichia albicollis
LeConte's sparrow	Ammodramus lecontii
red-winged blackbird	Agelaius phoeniceus
brown-headed cowbird	Molothrus ater
northern oriole	Icterus galbula
western tanager	Piranga ludoviciana
pine siskin	Carduelis pinus

Appendix 2. Summary of all species captured in mist nets, seen in clearcuts (within 100 m of the forest edge) or crossing Long Lake (Fig. 3-1), from Chapter 3. Superscripts denote location of capture and correspond to the following locations: 1 =West Buffer Treatment, 2 =West Buffer Control, 3= North Buffer Treatment, 4=North Buffer Control. Numbers reported include all first-time captures at all net lanes over all years, and total number of observations in clearcuts and the lake (likely non-unique individuals in some cases).

Species	*Scientific Name*	*No. of Adults Captured*		*No. of Juveniles Captured*		*No. Observervations*	
		Treat.	*Cont.*	*Treat.*	*Cont.*	*Clearcuts*	*Lakes*
Ruby-throated Hummingbird	*Archilochus colubris*	0	0	0	0	2	0
Yellow-bellied Sapsucker	*Sphyrapicus varius*	8^{1}	$7^{2,4}$	$11^{1,3}$	0	34	3
Hairy Woodpecker	*Picoides villosus*	1^{1}	0	0	0	11	3
Downy Woodpecker	*Picoides pubescens*	$2^{1,3}$	0	0	0	1	0
Three-toed Woodpecker	*Picoides tridactylus*	1^{1}	0	0	0	1	0
Northern Flicker	*Colaptes auratus*	0	0	0	0	8	4
Pileated Woodpecker	*Dryocopus pileatus*	0	0	0	0	0	1
Western Wood-pewee	*Contopus sordidulus*	2^{1}	0	0	0	0	0
Least Flycatcher	*Empidonax minimus*	$83^{1,3}$	$9^{2,4}$	2^{3}	2^{2}	3	0
Alder Flycatcher	*Empidonax alnorum*	0	1^{4}	0	0	1	0
Tree Swallow	*Tachycineta bicolor*	0	0	0	0	14	25
Barn Swallow	*Hirundo rustica*	0	0	0	0	0	3
Common Raven	*Corvus corax*	0	0	0	0	1	15
Blue Jay	*Cyanocitta cristata*	0	2^{2}	0	0	2	3
Gray Jay	*Perisoreus canadensis*	0	1^{2}	0	1^{4}	1	1
Black-capped Chickadee	*Parus atricapillus*	$8^{1,3}$	$10^{2,4}$	1^{1}	1^{2}	3	4
Brown Creeper	*Certhia americana*	0	1^{2}	0	0	1	0
Red-breasted Nuthatch	*Sitta canadensis*	0	$2^{2,4}$	0	1^{4}	0	0
House Wren	*Troglodytes aedon*	6^{3}	1^{4}	0	0	5	0
Winter Wren	*Troglodytes troglodytes*	0	0	0	1^{4}	0	0
Ruby-crowned Kinglet	*Regulus calendula*	1^{3}	1^{4}	0	0	0	0
American Robin	*Turdus migratorius*	4^{1}	$4^{2,4}$	0	2^{4}	16	3
Hermit Thrush	*Catharus guttatus*	$7^{1,3}$	$2^{2,4}$	2^{1}	$2^{2,4}$	0	0
Swainson's Thrush	*Catharus ustulatus*	$22^{1,3}$	$43^{2,4}$	$2^{1,3}$	$4^{2,4}$	1	0
Veery	*Catharus fuscescens*	1^{1}	0	0	0	0	0
Cedar Waxwing	*Bombycilla cedrorum*	$9^{1,3}$	1^{4}	0	0	178	67
Solitary Vireo	*Vireo solitarius*	0	1^{2}	0	0	0	0
Philadelphia Vireo	*Vireo philadelphicus*	4^{3}	0	0	0	0	0
Red-eyed Vireo	*Vireo olivaceus*	$2^{1,3}$	2^{2}	0	0	3	0
Warbling Vireo	*Vireo gilvus*	1^{3}	0	0	0	0	0
Tennessee Warbler	*Vermivora peregrina*	$3^{1,3}$	9^{4}	1^{1}	3^{4}	2	0
Black-and-white Warbler	*Mniotilta varia*	0	2^{4}	0	0	0	0
Yellow-rumped Warbler	*Dendroica coronata*	$15^{1,3}$	$21^{2,4}$	1^{3}	$4^{2,4}$	2	1
Black-throated Green Warbler	*Dendroica virens*	0	1^{4}	0	0	0	0
Yellow Warbler	*Dendroica petechia*	$16^{1,3}$	$2^{2,4}$	1^{1}	0	0	0
Mourning Warbler	*Oporornis philadelphia*	$23^{1,3}$	$6^{2,4}$	$5^{1,3}$	$3^{2,4}$	5	0
Connecticut Warbler	*Oporornis agilis*	3^{1}	3^{2}	$4^{1,3}$	0	4	0
Canada Warbler	*Wilsonia canadensis*	$6^{1,3}$	$13^{2,4}$	0	0	0	0
Wilson's Warbler	*Wilsonia pusilla*	0	2^{2}	0	0	0	0
Ovenbird	*Seiurus aurocapillus*	$26^{1,3}$	$25^{2,4}$	14^{1}	$5^{2,4}$	0	0

Appendix 2 continued

Species	*Scientific Name*	*No. of Adults Captured*		*No. of Juveniles Captured*		*No. Observervations*	
		Treat.	*Cont.*	*Treat.*	*Cont.*	*Clearcuts*	*Lakes*
Northern Waterthrush	*Seiurus noveboracensis*	1[3]	3[2]	1[1]	1[4]	0	0
Common Yellowthroat	*Geothlypis trichas*	1[1]	3[2,4]	0	0	2	0
American Redstart	*Setophaga ruticilla*	1[3]	2[4]	0	2[4]	0	0
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	1[1]	0	0	0	0	0
Sharp-tailed Sparrow	*Ammodramus caudacutus*	1[1]	0	0	0	0	0
Song Sparrow	*Melospiza melodia*	11[3]	8[2,4]	6[3]	3[2]	0	3
Chipping Sparrow	*Spizella passerina*	5[1]	8[2,4]	2[1]	0	33	4
Clay-colored Sparrow	*Spizella pallida*	0	0	0	0	6	0
Dark-eyed Junco	*Junco hyemalis*	0	4[2,4]	5[1]	8[2,4]	13	0
White-throated Sparrow	*Zonotrichia albicollis*	61[1,3]	30[2,4]	13[1,3]	4[2,4]	52	0
Lincoln's Sparrow	*Melospiza lincolnii*	17[1,3]	13[2,4]	0	4[2,4]	9	2
Swamp Sparrow	*Melospiza geogiana*	20[1,3]	2[4]	1[3]	0	0	2
Red-winged Blackbird	*Agelaius phoeniceus*	2[1]	0	0	0	47	68
Common Grackle	*Quiscalus quiscula*	0	0	0	0	0	2
Brown-headed Cowbird	*Molothrus ater*	0	0	1[3]	0	19	13
Northern Oriole	*Icterus galbula*	2[1,3]	0	0	0	1	0
Western Tanager	*Piranga ludoviciana*	7[1,3]	4[2,4]	2[1,3]	0	3	1
White-winged Crossbill	*Loxia leucoptera*	0	0	0	0	0	19
Purple Finch	*Carpodacus purpureus*	2[1]	0	0	0	2	0
Pine Siskin	*Carduelis pinus*	1[1]	0	0	0	65	13
Unknown sparrows						15	2
Unknown other						9	42
Totals		387	247	75	51	575	304

Appendix 3. Summary of protocol and results for Ovenbird pairing success at Calling Lake, Alberta, 1993 and 1994.

History

Ovenbirds are known to be sensitive to fragmentation in eastern North America (Robbins et al. 1989, Porneluzi et al. 1993). Previous studies that have compared pairing success in continuous woodlands to success in fragments (Gibbs and Faaborg 1990, Villard et al. 1993) found significant differences. Typically, pairing success ranged from 75 to 82% in continuous areas and fell to less than 60% in fragmented systems.

Methods

Male Ovenbird territories in forests near watercourses were delineated by spot mapping and additional field observation. The additional observation was time spent following males and observing countersinging, etc. Each male in the reserves connected by the west buffer, and the buffer, (see West Buffer, Fig. 3-1.) was observed in 1993. In 1994, additional males were observed as time permitted in other areas.

Direct observations of males were made until total observation time reached 60 minutes (track time), or until they were seen interacting with or within 5 m of a female Ovenbird (after Gibbs and Faaborg 1990). If no interaction occurred within 60 minutes of track time, the bird was classified as unpaired.

Results

The results have been summarized in Table (A3-1). Twelve of 14 males were paired prior to fragmentation (85.7%). Pairs were seen together in an average track time of 12.8 minutes. Following harvesting, 14 of 15 (93.3%) males seen in fragments in 1994 were paired. Average track time increased slightly to 17.4 minutes, due primarily to one outlier (Lloyd).

Discussion

Pairing success was not affected in the first year after disturbance of adjacent habitat. The degree of fragmentation may not currently be sufficient to affect the success of mate-finding in Ovenbirds. However, as the time since initial disturbance increases, the bird community adjusts to habitat alterations, and regional fragmentation increases, pairing success may eventually be affected as it has been in eastern North America.

Future investigators would do well to recognize several things that makes determining pairing success easier. First, observations should be made before the second week in June, or the time corresponding to egg laying. At this time the female spends considerable time away from the male who has no incubation duty. Pairs may not be discovered before 60 minutes track time elapses, biasing results. Also, the birds make a precopulatory trill that will alert the observer to the location of mating birds, speeding the process. Finally, finding Ovenbird nests is notoriously difficult, so any project proposing to do so will have to adjust expected sample sizes accordingly.

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Table A3-1. Identity, location and pairing status of Ovenbirds observed in 1993 and 1994.

Identity	Location†	Track Time	Status	Notes
		1993		
Terry & Rebecca	East of T-V in WB	17 min	Paired	
Earl & Melissa	NE of R-1-1 (overlaps)	11 min	Paired	
Lloyd	S portion of R-1-1	60 min	Bachelor	Sang frequently
Otis & Irene	S of R-1-1, E of buffer	5 min	Paired	
James & Helen	J3 in WB	2 min	Paired	Nest found, adults banded
Alex & Katrina	A1 in WB	38 min	Paired	
Larry	B5 in R-10-1	71 min	Bachelor	
Hans & Karen	near Buffer 3	4 min	Paired	
Norman & Penelope	NE corner of R-10-1	8 min	Paired	
Dick & Yvonne	D5-D7 in R-10-1	41 min	Paired	
Unnamed	γ11 in R-10-1	1 min	Paired	M-A; during spot map
Unnamed	Y in WB	<1 min	Paired	seen with young + mate
Unnamed	C11 in R-10-1	2 min	Paired	
Unnamed	E14 in R-10-1	24 min	Paired	
Victor & Martha	V in NB	2 min	Paired	North Buffer
Carl & Elizabeth	B to D in NB	13 min	Paired	North Buffer
Ziggy	Z in NB	21 min	Undetermined	North Buffer
Danny	DD-FF in NB	33 min	Undetermined	North Buffer
		1994		
Unnamed	A4-A3 in R-10-1	13 min	Paired	Key in '94 fieldbook for loc
Lloyd	R-1-2	83 min	Paired	Suspected paired @60
Unnamed	γ7 in R-10-1	35 min	Paired	
Unnamed	F-13, E11 R-40-2	3 min	Paired	
Unnamed	SW corner of R-40-2	6 min	Paired	
Unnamed	F-40-1 pt 1.1	2 min	Paired	
Unnamed	AA7 R-10-1	42 min	Paired	Nest at B7
Unnamed	5 ha frag	1 min	Paired	
Unnamed	Buffer 6	7 min	Paired	
Unnamed	R-40-3, near cabin	23 min	Paired	
Unnamed	AA11 R-10-1	1 min	Paired	
Unnamed	R-10-2, N of 1-0	60 min	Bachelor	
Unnamed	centre of R-10-2	5 min	Paired	
Unnamed	SW corner of R-10-2	22 min	Paired	
Unnamed	F-40-3, G4	1 min	Paired	Nest found
Unnamed	near C in WCB	1 min	Paired	Control forest
Unnamed	b/t F+H, WCB	1 min	Paired	Control forest

† WB = west buffer, WCB = west control buffer, NB = north buffer. Letter/number combinations refer to a position on the spot mapping grid of the particular area. The 5 ha fragment is the piece of forest east of R-40-2.